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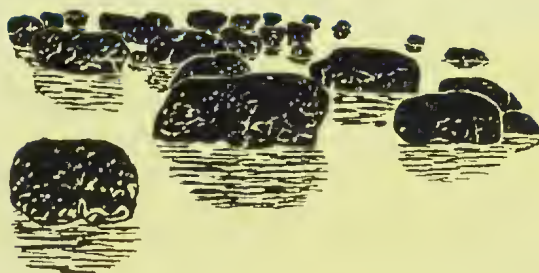


Journal of the Royal Society of Western Australia

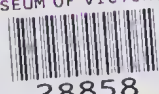
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Volume 78 Part 1
March 1995



MUSEUM OF VICTORIA



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ISSN 0035-922X

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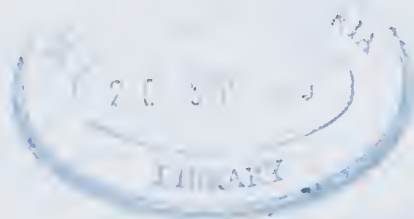
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June 1995

MUSEUM OF VICTORIA



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ISSN 0035-922X

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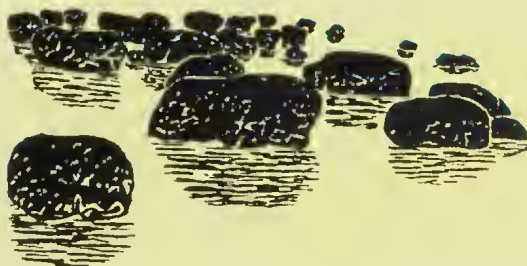


Volume 78 Part 3
September 1995

MUSEUM OF VICTORIA



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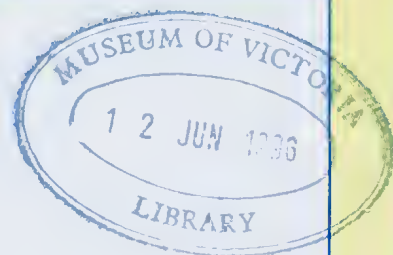
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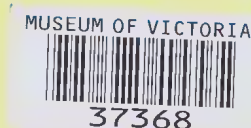
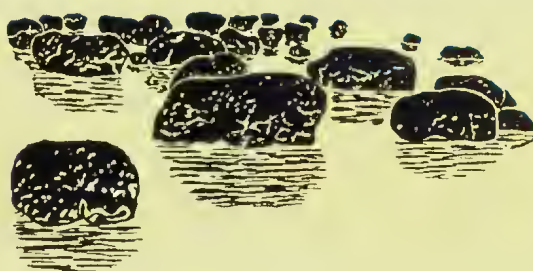
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December 1995



ISSN 0035-922X

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Recent Advances in Science in Western Australia

Earth Sciences

Twelve genera of chlorophycean algae in Triassic palynological assemblages from north-western Australia are reviewed by W Bremner (GEOMAR, Kiel) and C Foster (AGSO, Canberra). They suggest a possible evolutionary pathway for certain chlorococcalean coenobial families based on comparison with some living green algae (Orders Chlorococcales and Zygnematales) which develop resistant outer organic walls and/or cysts during their life cycle.

Brenner W & Foster C B 1994 Chlorophycean algae from the Triassic of Australia. Review of Paleobotany and Palynology 80:209-234.

Glengarry Group stratigraphy identified in the fold belt to the north can be applied to the southern foreland area on the Glengarry 1:250 000 map sheet. Four of the five major tectonic events that affected the Nabberu Province can be recognised on the foreland: listric faulting (Phase 1) relates to early basin subsidence by crustal extension; the succeeding convergent-styled Phases 2-4 (4 has no expression on the foreland) probably relate to the collision of the Capricorn Orogen; and the final tectonic act of normal faulting (Phase 5) may relate to the onset of crustal extension controlling the development of the younger Bangemall basin.

Gee R D & Grey K 1994 Proterozoic rocks on the Glengarry 1:250 000 sheet — stratigraphy, structure and stromatolite biostratigraphy. Geological Survey of Western Australia, Report 41.

Boudinage is shown by D Findlay (Consultant, South Perth) to be an important aspect of the structure of the goldfield, the lode distribution to be coincident with the principal necks, and the configuration of the lodes to match the characteristic fracture patterns of classical boudin necks. Boudinage is therefore interpreted to be an important control on the emplacement of mineralization and is proposed as a simpler alternative to the more complex shear-related models, and may be useful in exploration for deposits of similar type.

Findlay D 1994 Boudinage control on the emplacement of lodes of the Kalgoorlie goldfield. Australian Journal of Earth Sciences 41:105-113.

A U/Pb isotopic age determined by researchers from the Key Centre for Strategic Mineral Deposit Research (University of Western Australia) and the Research School of Earth Sciences (Australian National University), of 2991 ± 12 Ma, for zircons from the Mt Brown Rhyolite, in the Whim Creek Supersequence, supports previous evidence that the main periods of silicic volcanism in the west Pilbara are much younger than in the East Pilbara. Available data now favour the westwards growth of the Pilbara Craton from ca. 3.5 to 2.9 Ga, rather than the single essentially tabular stratigraphy for the craton originally proposed.

Barley M E, McNaughton N J, Williams I S & Compston W 1994 Geological note. Age of Archaean volcanism and sulphide mineralization in the Whim Creek Belt, west Pilbara. Australian Journal of Earth Sciences 41:175-177.

Studies of Archaean lode-gold deposits from Western Australia, by local scientists (Key Centre for Strategic Mineral Deposit Research, University of Western Australia) indicate that the Pb isotopic data distribution for ore-associated galenas and pyrites is commonly linear, and determination of the initial Pb ratio relies on selecting the least-radiogenic composition. Detailed studies of Victory Mine samples have led to the development of criteria for selecting target pyrite samples which best preserve the initial Pb ratio of the sulphide, and hence the ore fluid. The most important controls on the displacement of the measured Pb ratio of pyrite from the initial Pb ratio are the Pb content of pyrite, pyrite abundance, proximity of pyrite to ore-fluid channelway, and host rock.

Ho S G, McNaughton N J & Groves D I 1994 Criteria for determining initial lead isotopic compositions of pyrite in Archaean lode-gold deposits: a case study at Victory, Kambalda, Western Australia. Chemical Geology 111:57-84.

Life Sciences

Collaborative research, by scientists from James Cook University (Qld), Department of Conservation and Land Management (WA) and the Conservation Commission (NT), has examined the abundance and distribution of the dugong in Shark Bay, Western Australia. Aerial survey counts (corrected for perception and availability biases) indicated $10146 \pm se 1665$ individuals, at a density of $0.71 \pm se 0.12$ dugongs km^{-2} , with a high percentage of calves (19%). Shark Bay is confirmed to be an internationally significant dugong habitat.

Marsh H, Prince R I T, Saalfeld W K & Shepherd R 1994 The distribution and abundance of the dugong in Shark Bay, Western Australia. Wildlife Research 21:149-161.

A comparison by two South African scientists (Department of Botany, University of Cape Town) of plant traits for edaphically-matched sites at the Barrens, south-western Australia, and the Agulhas Plain, southwestern South Africa, indicated strong convergence in a wide range of traits related to morphology and function. Examples of non-convergence are attributed to regional and historical processes rather than differences in the contemporary physical environments of the two areas.

Cowling R M & Witkowski E T F 1994 Convergence and non-convergence of plant traits in climatically and edaphically matched sites in Mediterranean Australia and South Africa. Australian Journal of Ecology 19:220-232.

Bird censuses at 20 mulga sites across Australia enabled North American ornithologist, M Cody of the University of California at Los Angeles, to use null (binomial) models to show that community composition is far more consistent among censuses than expected at random. Of the total of 81 bird species censused, 32% were interpreted to be "core species" in "core niches" that accounted for almost 75% of the bird density in mulga communities. Regional variations in the composition of some guilds illustrated various factors that contributed to a large species total in mulga, despite the predominance of "core species"

Cody M L 1994 Mulga bird communities. I. Species composition and predictability across Australia. Australian Journal of Ecology 19:206-219.

A study of the parrotfish family (Scaridae) by D Bellwood uses comparative morphology to identify species groups within the family, and determine their phylogenetic relationships. Examination of 143 character states for 69 of the 180 species of Scaridae are used for analysis by the principal of maximum parsimony. A diagnosis of supraspecific taxa, a key to genera, and a list of Recent species are also provided.

Bellwood D R 1994 A phylogenetic study of the parrotfishes family Scaridae (Pisces: Labroidae), with a revision of genera. Records of the Australian Museum. Supplement 20.

Researchers from the CSIRO Tropical Ecosystems Research Centre (NT) and Harvard University (USA) used an experimental study of the influence of abundance, high activity, and aggressiveness of Australian meat ants to demonstrate that their interference with other ant species has important implications for the sizes and densities of colonies of the other species, and ultimately the overall ant community structure.

Andersen A N & Patel A D 1994 Meat ants as dominant members of Australian ant communities: an experimental test of their influence on the foraging success and forager abundance of other species. *Oecologia* 98:15-24.

The structure and fecundity of *Banksia menziesii* varies between its mesic range (Swan Coastal Plain) where the tree form has a relatively low fecundity, and its xeric range (Eneabba Plain) where the shrub form has a higher fecundity. Plants on road verges had a larger crown and a higher fecundity than plants more than 50 metres from the verge.

Lamont B B, Whitten V A, Witkowski E T F, Rees R G & Enright N J 1994 Regional and local (road verge) effects on size and fecundity in *Banksia menziesii*. *Australian Journal of Ecology* 19:197-205.

Study of algal zonation on the intertidal limestone platforms off Perth by R Scheibling, of Dalhousie University, Halifax, indicates a characteristic pattern of

dense macroalgal beds nearshore with a barren zone on the seaward edge. Manipulative experiments indicated that the extent of algal cover was inversely related to the numbers of grazing molluscs, and that limpets and chitons accounted for 55 to 89% of the variation in algal cover whereas abalone accounted for <10%. The effect of the grazers was both through decreased space for colonization by algae due to the home scar area of the molluscs, and by grazing around the home scar area.

Scheibling R E 1994 Molluscan grazing and macroalgal zonation on a rocky intertidal platform at Perth, Western Australia. *Australian Journal of Ecology* 19:141-149.

Note from the Hon Editor: This column helps to link the various disciplines and inform others of the broad spectrum of achievements of WA scientists (or others writing about WA). Contributions to "Recent Advances in Science in Western Australia" are welcome, and may include papers that have caught your attention or that you believe may interest other scientists in Western Australia and abroad. They are usually papers in refereed journals, or books, chapters and reviews. Abstracts from conference proceedings will not be accepted. Please submit either a reprint of the paper, or a short (2-3 sentences) summary of a recent paper together with a copy of the authors' names and addresses, to the Hon Editor or a member of the Publications Committee: Dr S D Hopper (Life Sciences), Dr A E Cockbain (Earth Sciences), and Assoc Prof G Hefter (Physical Sciences). Final choice of articles is at the discretion of the Hon Editor.

"Letters to the Editor" concerning scientific issues of relevance to this journal are also published, at the discretion of the Hon Editor. Please submit a word processing disk with letters, and suggest potential reviewers or respondents to your letter. *P C Withers, Hon Editor, Journal of the Royal Society of Western Australia.*

The role of diet in determining water, energy and salt intake in the thorny devil *Moloch horridus* (Lacertilia: Agamidae)

P C Withers¹ & C R Dickman²

¹Department of Zoology, University of Western Australia, Nedlands WA 6907

²School of Biological Sciences, University of Sydney, Sydney NSW 2006

Manuscript received June 1994; accepted October 1994.

Abstract

We examine the nutritional and digestive constraints of obligate myrmecophagy to the Australian agamid lizard, the thorny devil *Moloch horridus*. Observations of thorny devils feeding in their natural habitat, and examination of faeces collected from their habitat, confirm their essentially myrmecophagous diet. We identify two common types of ants that are eaten by thorny devils, *Iridomyrmex* sp from terrestrial trails, and *Crematogaster* sp from trails along the stems of currant bush (*Leptomeria preissiana*). Ants are consumed at a variable rate, from about 1 min⁻¹ to 12 min⁻¹. The water, energy and solute content of ants is similar to other insects; the *Iridomyrmex* sp and *Crematogaster* sp were 62% water, and contained on a dry-mass basis 28-29 kJ g⁻¹, 130-180 µmol Na⁺ g⁻¹, and 220-240 µmol K⁺ g⁻¹. The movements of thorny devils encompassed a variable area; lizards often remained within a restricted area over short periods, and did not exhibit any apparent signs of territoriality. Some lizards remained in restricted areas over considerable periods (6 months to >1 year) whereas others dispersed widely. Thorny devils were observed to be active, and feeding, over a wide range of body temperatures, and their foraging did not appear to be related to, or restricted by, any particular body temperature. The digestive assimilation of thorny devils maintained in the laboratory was only 37% for dry matter, and 59% for metabolisable energy; the expected metabolisable energy efficiency is about 70% for a generalised insect diet, but would be expected to be lower for heavily sclerotised insects, such as ants. Our analyses of the nutritional value of ants, the measured metabolisable energy efficiency, and the assumption that thorny devils consume about 750 ants per day, indicate a field water turnover rate of 0.3 ml d⁻¹, and a field metabolic rate of 2.7 kJ d⁻¹. This calculated water turnover rate is considerably lower than expected for a 35 g lizard, but is similar to that measured by radio-isotopic turnover for thorny devils in the field (Withers & Bradshaw 1995). The calculated field metabolic rate is slightly less than that predicted for a 35 g lizard, and is similar to that measured for thorny devils in the field (Withers & Bradshaw 1995). We conclude that naturally-feeding thorny devils probably consume about 750 ants per day.

Introduction

The thorny devil, or mountain devil, (*Moloch horridus*) is an extremely cryptic, slow-moving agamid lizard that is wide-spread throughout much of semi-arid and arid Australia (Greer 1989; Cogger 1992). It is a sit-and-wait predator of small ants, primarily *Iridomyrmex* spp (Saville-Kent 1897; Davey 1923, 1944; White 1947; Sporn 1955; Paton 1965; Pianka & Pianka 1970). However, little is known of the natural history, ecology or physiology of the thorny devil (Bentley & Blumer 1962; Pianka & Pianka 1970; Gans et al. 1982; Sherbrooke, 1993; Withers 1993; Heatwole & Pianka 1993; Whitten 1993), in part because it is very cryptic and difficult to study in the field.

Some other Australian lizards, particularly dragons, opportunistically consume ants but none are so exclusively ant-consumers as is the thorny devil (Pianka & Pianka 1970; Pianka 1986). Many consume termites

opportunistically, and some geckos (*Diplodactylus conspicillatus* and *Rhynchoedura ornata*) and skinks (*Ctenotus* spp) are termite specialists (Pianka 1969). Food specialisation on social insects such as ants and termites may be advantageous because the prey are a clumped and concentrated food supply, but the nutritional and energetic consequences of a restricted diet such as ants or termites have been poorly addressed even for other taxa of ant-eaters such as mammals. For example, Redford & Dorea (1984) suggested that the low nutritional value of termites and especially of heavily sclerotised ants is a disadvantage (although alates have an exceptionally high nutritional value). The nitrogen levels of ants and termites are not particularly unusual, compared to other invertebrates, but Phelps *et al.* (1975) reported a low digestibility by rats for termite protein. We are unaware of any studies which have determined for myrmecophages the digestive assimilation efficiency for either dry matter or energy.

In this study, we document the composition of the diet for thorny devils at a study site located north of

Southern Cross, Western Australia. We measure the water, energy, sodium and potassium contents for the ant fauna at this study site, and we determine the digestive efficiency of thorny devils for *Iridomyrmex* sp in the laboratory. In addition, we examined thermoregulation and movements of thorny devils. These studies enable us to evaluate possible hygric, energetic, ionic, thermoregulatory and locomotory constraints of myrmecophagy for free-living thorny devils, and to estimate values for, and ratios of, water, energy and solute turnovers.

Methods

Field Site

Thorny devils were observed and studied in the field, in a sandplain habitat (latitude 30° 17'S, longitude 119° 44'E; Fig 1) located 10-20 km north of Bungalbin, Western Australia (near fauna site 39 of Dell *et al.* 1985). The vegetation was spinifex (*Triodia scariosa* and *Plechtrachne* sp) mixed with *Eucalyptus leptopoda* mallee and *Banksia elderana*, *Acacia coolgardiensis* and *Callitris preissii* tall shrubland (Dell *et al.* 1985; Beard 1990). Currant bush (*Leptomeria preissiana*; Fig 2A) was also present in the north-easterly parts of the study site. The study area is sub-desert, with warm winters (July, average monthly maximum 16-17°C) and hot summers (January, average monthly maximum 34-36°C); average annual rainfall is about 265 mm, with January-August being the wettest months (Dell *et al.* 1985).

Thorny devils were routinely captured by pit-trapping, using 0.5 m long PVC pipe pit traps (160 mm dia) and aluminium flywire fences. Individuals were also located opportunistically by walking through the study area and examining the base of currant bushes where thorny devils were often seen feeding on arboreal ants. Their faeces were collected opportunistically in the field; the characteristic size and appearance, as well as their



Figure 1. Location of field study site.

almost exclusive ant content, readily identified *Moloch* faeces. Faeces were often located in aggregations of 5 to 20 individual pellets.

Observations of *Moloch* feeding undisturbed at the study site enabled identification of their common ant prey as the numerous small terrestrial *Iridomyrmex* sp, as well as an ant (*Crematogaster* sp) common on currant bush. Individuals of these ant species, and numerous other species from the study site, nearby locations, and



Figure 2. A (left): Typical habitat of thorny devils in the sandplain, showing a currant bush (*Leptomeria preissiana*). B (right): Characteristic feeding posture of a thorny devil consuming ants from a trail on the trunk of a currant bush.

Perth, were sampled for identification and determination of water, energy and solute content. Ants were collected and placed in sealed plastic vials, and frozen for return to the laboratory for analysis.

Movements of thorny devils

The daily movements of thorny devils were monitored by thread spool and radiotelemetry, and longer term movements were monitored by recapture of marked (toe-clipped) individuals at the study site. A centre-unwinding nylon thread spool (Penguin Thread Company; 2 grams; ≈ 270 m total length) was taped to the dorsal surface of the tail of some thorny devils. The centre-unwinding, free end of the thread was tied to a marker stake, and the lizard was able to walk unhindered by the thread trail. The length of thread that was unwound by the lizards movements was determined by following the thread and rewinding it to the current location of the lizard, then measuring the length of retrieved thread in the laboratory. This technique determines the actual daily distance moved by the lizard. Small radiotelemeters (Biotrack SS-1 one-stage; ≈ 1 g) were taped to the dorsal surface of the tail of some thorny devils. These lizards were generally relocated daily using a Biotelemetry Systems radioreceiver and hand-held antenna. The actual location of the lizard was marked with a stake, and the distance and direction to the previous location were measured. Daily relocation allowed the determination of the daily point-to-point movement of lizards, and the average daily point-to-point movement over a period of 7 to 14 days. Thorny devils were marked on the abdomen using a felt-tip pen for a short-term identification, and many were marked permanently by toe-clipping.

Composition of ants

Ants were weighed individually, or in groups of 5 to 10 for smaller individuals, to ± 0.0001 g, then oven-dried at 60°C to determine water content. The dried bodies were then analysed either for energy or solute content.

The energy content of 5 to 20 mg of dried ant bodies was determined using a microbomb calorimeter (Phillipson 1964) calibrated using oven-dried benzoic acid. It was not possible to determine the ash content of samples, so all energy values for ants are expressed as kJ per gram total dry mass.

The sodium and potassium contents of ant bodies were determined by digesting the oven-dried bodies in 0.5 to 1.0 ml of 10N nitric acid, then measuring the sodium and potassium ion contents of the digested supernatant with a Varian atomic absorption spectrophotometer, using caesium chloride as an internal standard.

Feeding trials

Thorny devils were returned to the laboratory in Perth, and fed daily with locally-collected *Iridomyrmex* ants. The lizards were housed in the laboratory in glass aquaria, with a dry sandy substrate, and a heat lamp for thermoregulation during the day. It proved impossible to feed the lizards with known numbers of weights or live ants, and so lizards were weighed to ± 0.0001 g then placed in an aquarium containing freshly-collected ants, and allowed to feed for approximately 30 min, when they were removed and reweighed to determine the

mass of ants consumed. The thorny devils were maintained in the laboratory for 5 to 20 days in this fashion. Faeces were collected daily and oven-dried and stored for weighing and analysis of energy content.

The dry matter and energy content of the ants was determined as described above. The energy content of 0.5 to 1.5 gram samples of faeces was determined using a Gallenkamp bomb calorimeter, calibrated using benzoic acid. The ash and sand content of the faeces was determined by weighing the sample crucible before and after bombing. Energy values for faeces are presented as kJ per total dry weight (to calculate the total energy content of collected faeces) and kJ per ash-free dry weight (for comparison with the energy content of ants). The uric acid components of the faeces were included in energy determination; the "faecal" mass and energy loss therefore included material/energy that was absorbed from the digestive tract but was subsequently excreted (e.g. urine), material/energy that was not absorbed from the digestive tract but eliminated as faeces, and material/energy added to the digestive tract e.g. secretions and sloughing of the gut lining. This was done because it was considered important to determine the overall material and energy balance of the diet, for comparison with a study of field metabolic rate of thorny devils (Withers & Bradshaw, 1995).

Body Temperature

When thorny devils were located in the field, their body temperature (T_b ; $^\circ\text{C}$) was measured immediately before disturbance whenever possible, using a Schultheis cloacal thermometer; air temperature (T_a ; 1 m above ground in the shade) and substrate temperature (T_s) at the site where the thorny devil was first observed were also measured.

Thorny devils were routinely maintained in the laboratory in a large circular tank (dia = 3 m), with access to a heat lamp. Body temperature was determined for devils at various times throughout the day, using a Schultheis cloacal thermometer.

Results

Diet of thorny devils

Observation of thorny devils, feeding naturally in the field, indicated that lizards typically positioned themselves over or just to the side of an ant trail, either on a sandy area or at the base of a currant bush (Fig 2B), and repetitively captured passing ants using their tongue. The ants that were observed to be eaten were invariably the common, small species; ants taken from the ground were *Iridomyrmex* sp, and ants from the currant bush were *Crematogaster* sp. The *Iridomyrmex* were readily distinguishable from *Crematogaster*, which had a very spinous trunk, with two distinctive posteriorly-directed spines on the propodeum, and a "heart"-shaped abdomen.

Feeding rates observed for thorny devils in the field varied markedly from <1 to >10 ants min^{-1} (individual values were; 0.6, 2, 2, 2, 3.3, 7.7, and 6-12 min^{-1}); mean 2.9 min^{-1} . Over short periods, however, rates up to 1 sec^{-1} were recorded; this is the maximum possible rate

because it took about 1 sec for a thorny devil to locate, capture and swallow an ant. The feeding rate appeared to vary with the abundance of ants and ambient temperature. Captive thorny devils were observed to feed at ant trails of *Iridomyrmex* spp in Perth at a rate of 0.5 to 5.8 min⁻¹ (0.5, 1.3, 1.4, 2.6, 2.9, 3.1, 3.7, 4.3, 4.5, 4.7, 5.8 min⁻¹); mean = 2.7 min⁻¹.

The faeces of *Moloch horridus* are quite distinctive, being large, ovoid and glossy in appearance; a urate pellet is frequently attached to one end of the faecal pellet (Fig 3A). The presence of essentially 100% ants in the diet is readily confirmed by visual inspection of crushed faecal pellets. Microscopic examination of faeces collected from the field confirmed the presence in the diet of small *Iridomyrmex* in localities without currant bush, and of mainly *Crematogaster* in localities with currant bush (Fig 3B). In addition, pieces of charcoal (Fig 3C) and occasionally small pieces of vegetation (Fig 3D) were frequently found in the faeces. Presumably the latter items were either ingested through mistaken identity with small black ants (*i.e.* charcoal pieces) or perhaps as items being carried by ants (*i.e.* plant material).

In addition to the common *Iridomyrmex* sp and *Crematogaster* sp consumed by thorny devils, a number of other ant species were collected from the ground and bushes at the study site, and other sites in the wheatbelt and in Perth.

Ant composition

The body mass (fresh) of ants varied considerably (Table 1), from less than 0.5 mg per individual, to over 100 mg per individual. The commonly-consumed *Iridomyrmex* (species 2) were about 0.45 mg, and the *Crematogaster* were slightly larger at 1.2 mg per individual.

The water contents of the various ants ranged from less than 50% to over 80%. There were highly significant differences in water content between the various species of ants (for species with $n > 2$; ANOVA; $F_{13,168} = 39$; $P < 0.0005$). The commonly-consumed *Iridomyrmex* 2 and *Crematogaster* sp (62% water) had an intermediate water content (Table 1). The energy content of the ants, expressed per g total weight, ranged from less than 20 to more than 30 kJ g⁻¹; the *Iridomyrmex* 2 and *Crematogaster* were intermediate, at 28 and 29 kJ g⁻¹ respectively. There were highly significant differences in energy contents of the various ant species ($n > 2$; ANOVA; $F_{13,57} = 4.8$; $P < 0.0005$). The sodium and potassium contents of the various ant species were quite variable, ranging from less than 100 to over 300 $\mu\text{mol g dry mass}^{-1}$, with highly significant differences observed between species for both sodium ($n > 2$; ANOVA; $F_{10,41} = 4.8$; $P < 0.0005$) and potassium ($n > 2$; ANOVA; $F_{10,39} = 8.5$; $P < 0.0005$). The commonly-consumed *Iridomyrmex* 2 and *Crematogaster* sp had typical sodium contents (179 and 126 $\mu\text{mol g dry mass}^{-1}$).

Table 1

Mean body mass and water, energy, sodium and potassium contents for various species of ants. The species observed to be eaten by thorny devils are indicated by an asterisk, and values are in bold face. Values are mean $\pm$ standard error, with the number of observations in parentheses.

Species	Mass mg Dry mass	Water Content %	Energy Content kJ g ⁻¹ Dry mass	Sodium Content $\mu\text{mol g}^{-1}$ Dry mass	Potassium Content $\mu\text{mol g}^{-1}$ Dry mass
not identified	10.6 (2)	72.2 (2)	27.7 (1)	219 (1)	268 (1)
not identified	26.5 (2)	71.0 (2)	24.6 (1)	211 (4)	231 (1)
<i>Aphaenogaster</i> 1	1.5 $\pm$ 0.1 (4)	72.9 $\pm$ 0.6 (4)	32.0 (2)	163 (1)	195 (1)
<i>Camponotus</i> sp	8.7 (1)	66.7 (1)			
<i>Camponotus</i> sp	14.2 (2)	67.8 (2)	18.6 (1)	233 (1)	181 (1)
<i>Camponotus</i> sp	4.0 $\pm$ 0.2 (5)	68.0 $\pm$ 2.0 (5)	22.5 (2)	131 (2)	174 (2)
<i>Camponotus</i> 1	6.9 $\pm$ 0.3 (10)	65.9 $\pm$ 0.9 (10)	22.7 $\pm$ 1.9 (5)	163 $\pm$ 17 (5)	255 $\pm$ 15 (5)
<i>Camponotus</i> 2	5.35 $\pm$ 0.4 (10)	60.0 $\pm$ 0.9 (10)	24.5 $\pm$ 2.3 (7)	$\pm$ 97 (2)	171 (2)
<i>Camponotus</i> 3	19.3 $\pm$ 0.8 (3)	74.1 $\pm$ 1.6 (3)	18.1 (1)	328 (1)	344 (1)
<i>Crematogaster</i> sp*	1.2 $\pm$ 0.1 (7)	62.0 $\pm$ 2.5 (7)	29.2 $\pm$ 1.2 (4)	126 (2)	216 (2)
<i>Iridomyrmex</i> sp	2.45 (2)	68.5 (2)	39.2 (2)		
<i>Iridomyrmex</i> sp	1.8 $\pm$ 0.2 (5)	53.8 $\pm$ 1.7 (5)	17.8 $\pm$ 0.9 (3)	127 (2)	149 (2)
<i>Iridomyrmex</i> 1	0.71 $\pm$ 0.03 (7)	63.2 $\pm$ 1.4 (7)	26.7 $\pm$ 1.3 (3)	213 $\pm$ 31 (3)	240 $\pm$ 36 (3)
<i>Iridomyrmex</i> 2*	0.45 $\pm$ 0.03 (13)	62.1 $\pm$ 1.4 (13)	28.1 $\pm$ 3.4 (4)	179 $\pm$ 41 (5)	241 $\pm$ 32 (5)
<i>Iridomyrmex</i> 3	0.38 (2)	68.4 (2)	22.5 (1)	237 (1)	275 (1)
<i>Iridomyrmex</i> 4	6.43 $\pm$ 0.3 (6)	70.5 $\pm$ 0.8 (6)	31.0 $\pm$ 1.0 (3)	252 $\pm$ 29 (3)	253 $\pm$ 13 (3)
<i>Iridomyrmex</i> 5	0.9 $\pm$ 0.04 (14)	65.5 $\pm$ 1.0 (12)	30.8 $\pm$ 0.7 (6)	126 $\pm$ 12 (4)	160 $\pm$ 7 (4)
<i>Iridomyrmex</i> agilis	0.77 $\pm$ 0.04 (3)	41 $\pm$ 3.2 (3)	31.5 (1)	56 (1)	40 (1)
<i>Iridomyrmex</i> purpureus	10.5 $\pm$ 0.1 (20)	70.1 $\pm$ 0.5 (20)	22.9 $\pm$ 0.9 (7)	243 $\pm$ 39 (6)	227 $\pm$ 16 (6)
<i>Melophorus</i> sp	29.1 $\pm$ 1.4 (4)	63.6 $\pm$ 2.9 (4)	22.4 (1)	101 (1)	162 (1)
<i>Meranoplus</i> sp	1.3 $\pm$ 0.1 (4)	64.4 (1)	27.1 (1)	34 (1)	43 (1)
<i>Pheidole</i> sp	0.27 (1)	51.9 (1)	21.5 (1)		
<i>Polyrachis</i> sp	12.2 $\pm$ 0.8 (20)	70.1 $\pm$ 0.5 (19)	26.0 $\pm$ 0.8 (7)	120 $\pm$ 10 (6)	162 $\pm$ 15 (4)
<i>Rhytidoponera</i>	14.9 (1)	58.4 (1)		164 (1)	167 (1)
<i>Rhytidoponera</i> 1	29.1 $\pm$ 2.1 (15)	58.5 $\pm$ 0.4 (15)	23.4 $\pm$ 0.7 (7)	115 $\pm$ 10 (6)	133 $\pm$ 13 (6)
<i>Rhytidoponera</i> 2	6.4 $\pm$ 0.6 (17)	53.4 $\pm$ 0.6 (17)	28.7 $\pm$ 1.0 (7)	115 $\pm$ 12 (5)	149 $\pm$ 9 (5)
<i>Rhytidoponera</i> 3	12.8 $\pm$ 0.5 (7)	54.9 $\pm$ 1.2 (7)	25.8 $\pm$ 0.7 (4)	108 $\pm$ 19 (3)	152 $\pm$ 9 (3)
<i>Rhytidoponera</i> 4	36.6 $\pm$ 1.5 (20)	57.8 $\pm$ 0.9 (20)	25.3 $\pm$ 1.8 (4)	115 $\pm$ 13 (6)	127 $\pm$ 13 (6)

mass⁻¹ respectively) and potassium contents (241 and 216 $\mu\text{mol g dry mass}^{-1}$ respectively).

Movements of thorny devils

The pattern of movements by thorny devils was variable; some lizards moved infrequently and for relatively

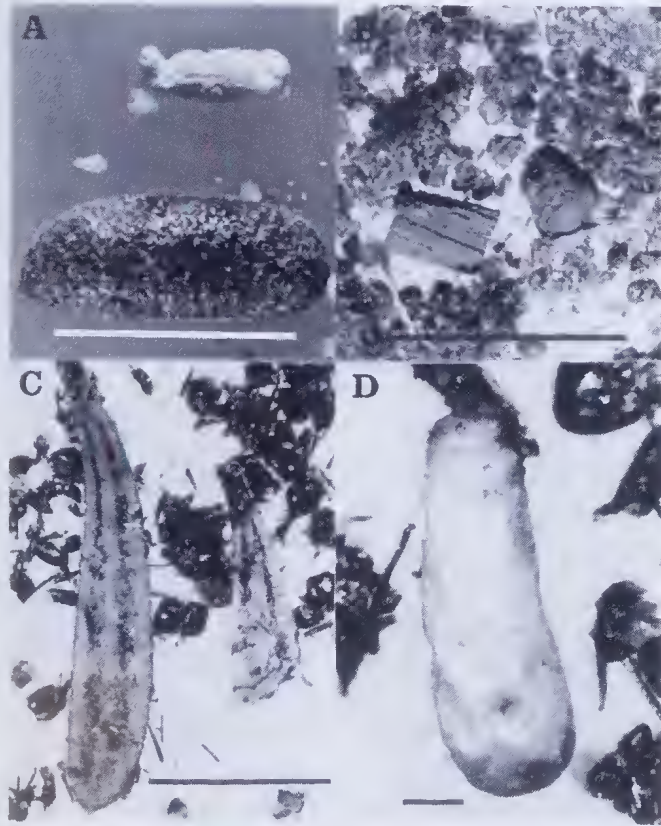


Figure 3. A: The glossy, ovoid faecal pellet of a thorny devil, showing the attached uric acid aggregate. (scale bar = 1 cm) B: Typical view of the contents of the faecal pellet of a thorny devil, showing numerous pieces of ant exoskeleton and a charcoal granules. (scale bar = 5 mm) C, D: Parts of vegetation from a faecal pellet. (scale bar = 1 mm)

short distances (10–20 m day⁻¹) whereas others moved more often and for greater distances (>100 m day⁻¹). A few individuals moved further than the length of a nylon spool (≈ 270 m), or beyond radio-tracking range (≈ 500 m) in a single day, and are necessarily excluded from numerical analysis here. The pattern of movement of individuals (e.g. Fig 4) does not suggest any maintenance of exclusive home ranges, since the movements of many lizards overlapped those of others. Occasionally, two lizards were found together. The actual distance moved per day by thorny devils with spools was 77.9 m day^{-1} ($\pm \text{se } 8.2$; $n=13$). The direct distance moved per day by radio-tracked thorny devils between daily relocation sites was $45.6 \text{ m point-to-point day}^{-1}$ ($\pm \text{se } 8.6$; $n=10$). The net distance moved per day between the first and final relocation sites (determined over 7 to 14 days) was only 16.6 m day^{-1} ($\pm \text{se } 3.9$; $n=14$). All of these values are significantly different (ANOVA, $F_{2,34} = 20$, $P < 0.001$; Newman-Keul's multiple comparison test).

A number of thorny devils were recaptured between field trips, within about 100 m of the same location, after periods of 6 months (8 individuals), about 1.5 years (3), 2 years (1), and 3 or more years (3). One had moved 0.4 km after 4 months, five had moved about 1 km after 6 months to 1 year, two had moved about 2.5 km after 4 years, and one had moved about 8 km after 1.5 years.

Digestion trials

Ten thorny devils were studied in the laboratory (body mass = $28.6 \pm \text{se } 3.7 \text{ g}$; range 15 to 52 g). The ants fed to thorny devils in the laboratory (*Iridomyrmex* 5) consisted of 65.5% water and contained 30.8 kJ of energy per g total wet weight (Table 1). The faeces of thorny devils had an energy content of $7.80 \pm 0.47 \text{ kJ g}^{-1}$ ($n=24$) expressed per total dry mass (including adherent sand particles) and $19.9 \pm 0.62 \text{ kJ g}^{-1}$ ($n=22$) expressed per ash-free dry mass. The mean ash content of faeces was very high, $37.1 \pm 1.5\%$ (24), presumably because of their high sand content, both grains within and adherent to the outside of the faecal pellet.

The thorny devils consumed ants at a rate of 0.16 ± 0.02 ($n=10$) g wet mass d⁻¹ (or 0.057 ± 0.01 g dry mass d⁻¹), which is about 0.6% of their body mass per day. This is equivalent to a total energy intake of 1.8 kJ day^{-1} . No thorny devils consumed sufficient ants per day to maintain a constant body mass; the observed weight change of -0.13 g d^{-1} ($\pm \text{se } 0.02$) was significantly different from 0 ($t_9 = 6.5$, $P < 0.001$). However, this was significantly less ($t_{14} = 8.4$, $P < 0.001$) than the weight loss of non-feeding thorny devils of -0.30 g d^{-1} ($\pm \text{se } 0.06$, $n=6$).

For five thorny devils, sufficient faeces were collected to enable a meaningful estimation of their steady-state energy assimilation. The total dry weight of faeces excreted over the duration of the feeding trials was $0.098 \pm 0.022 \text{ g d}^{-1}$ and the ash-free dry weight was $0.036 \pm 0.008 \text{ g d}^{-1}$. The calculated metabolisable dry matter assimilation was 37%, but the food intake was not expressed as ash-free mass whereas the faecal energy was expressed as ash-free mass (to account for its high sand and other inorganic material content). The calculated metabolisable energy assimilation was 59%, which was considerably higher than the metabolisable dry matter assimilation. The metabolisable energy intake of the thorny devils was

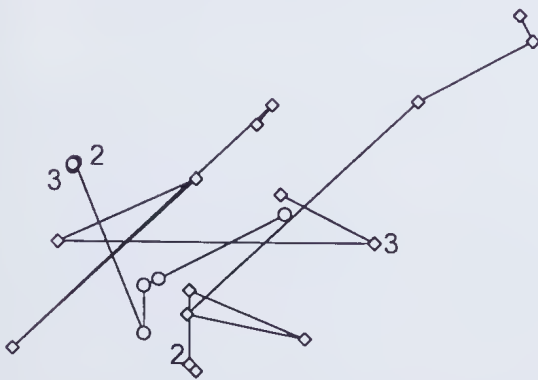


Figure 4. Pattern of movements of thorny devils. Axis tick marks are 20m intervals. Numbers next to location points (O) indicate the number of consecutive days that the lizard was located in that place (if >1).

consequently 1.0 kJ day^{-1} (or $0.072 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$; assuming $20.1 \text{ J} \equiv 1 \text{ ml O}_2$).

Body Temperature

The mean body temperature of thorny devils able to thermoregulate behaviourally in the laboratory was 34.5°C ($\pm \text{sd } 2.43$; $\pm \text{se } 0.48$; $n=26$); the body temperature data were slightly negatively skewed, with a median value of 34.0°C (Fig 5).

The average for all field body temperatures recorded for thorny devils was 28.3°C ($\pm \text{sd } 6.6$; $\pm \text{se } 0.7$; $n=93$), but ranged widely from 14.5°C to 38.7°C . Mean air temperature was 25.6°C ($\pm \text{sd } 5.8$; $\pm \text{se } 0.6$; $n=93$), and ranged widely from 16.0°C to 40.9°C (Fig 5). Mean substrate temperature was 24.5°C ($\pm \text{sd } 6.5$; $\pm \text{se } 0.8$; $n=93$), and ranged widely from 14.0°C to 41.7°C . There was a significant linear regression relationship between all T_b and T_a data, and all T_b and T_s data;

$$T_b = 4.1 (\pm \text{se } 1.8) + 0.95 (\pm \text{se } 0.07) T_a \quad (n=92; r^2 = 0.68; P < 0.001)$$

$$T_b = 5.9 (\pm \text{se } 1.7) + 0.88 (\pm \text{se } 0.07) T_s \quad (n=67; r^2 = 0.73; P < 0.001)$$

However, further analysis of the T_b and T_a data using two regression analysis to minimise the total residual sum of squares (Withers 1981; Yeager & Ultsch 1989; Fig 5) indicated separate relationships for $T_b < 32.5^\circ\text{C}$ and $T_b > 32.5^\circ\text{C}$; for $T_b < 32.5^\circ\text{C}$,

$$T_b = -0.6 (\pm \text{se } 1.8) + 1.10 (\pm \text{se } 0.08) T_a \quad (n=62; r^2 = 0.77; P < 0.001)$$

and for $T_b > 32.5^\circ\text{C}$,

$$T_b = 29.5 (\pm \text{se } 1.7) + 0.20 (\pm \text{se } 0.06) T_a \quad (n=27; r^2 = 0.34; P < 0.001)$$

At the highest T_a 's, three thorny devils were captured in or near burrows; their T_b was lower than the T_a (Fig 5).

Discussion

Our observations of the diet of thorny devils are consistent with previous reports of their essentially being

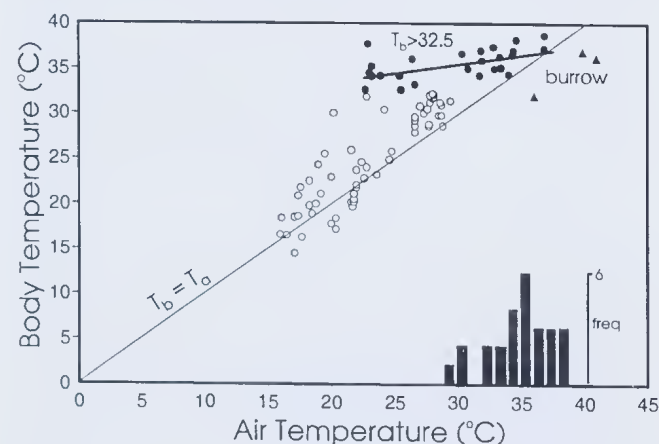


Figure 5. Relationship between body temperature and ambient air temperature for thorny devils in the field. Circles indicate data for surface active lizards; triangles are data for animals found in burrows. Closed circles and regression line are for lizards with $T_b > 32.5^\circ\text{C}$ (see text).

entirely myrmecophagous (e.g. Saville-Kent 1897; Pianka & Pianka 1970). We have observed thorny devils to consume ants (*Iridomyrmex* sp) not only from terrestrial trails, but also *Crematogaster* sp from trails along the trunks of currant bushes, by standing next to or propped against the trunk with their forelegs (Fig 2B). Davey (1923, 1944) reported that thorny devils were selective for *Iridomyrmex rufoniger* over other *Iridomyrmex*, *Ectatomma*, *Monomorium*, *Camponotus*, *Polyrhachis* and *Pheidole* species. Sporn (1955) recorded that thorny devils would eat six species of non-stinging ants. Pianka & Pianka (1970) reported the contents of thorny devil stomachs to consist mainly of small (2 to 5 mg) *Iridomyrmex*, and some sticks, stones, small flowers and insect eggs, presumably ingested coincidentally with ants or by mistake.

The faeces of thorny devils are quite characteristic, being large, ovoid pellets often with an adhering uric acid aggregate (Pianka & Pianka 1970; Fig 3A). The faeces are often found in groups of a few to over twenty pellets, varying from obviously fresh to much older ones. These aggregations of faeces in special "latrine" sites occur separately from basking sites (Pianka & Pianka 1970), and indicate either the activities of a single individual over a considerable time, the combined activities of a number of individuals, or both. The faeces of thorny devils from our study localities with currant bush contained numerous fragments of *Crematogaster* sp, whereas faeces from other nearby localities without currant bush consisted of mainly fragments of *Iridomyrmex* sp. Thus, it appears that thorny devils will vary their feeding strategy and the species of ant that they feed on, depending on local conditions, but concentrate on relatively small and abundant ants which form trails. The other species of ants which we collected in the vicinity of the field site were not consumed, at least in significant numbers, presumably because of their unsuitable size, low abundance, or non-trailing behaviour.

All previous reports of feeding rates have been for captive thorny devils. Saville-Kent (1897) reported that thorny devils consumed about 1000 to 1500 *Iridomyrmex* per meal, from ant trails. Davey (1923, 1944) reported that thorny devils consumed ants at a rate of about 45 min^{-1} , in probably two meals per day lasting about 15 min each, which was sufficient to satiate the thorny devils; consequently, the ingestion of ants was about 1350 individuals day^{-1} . Similar rates of feeding were reported also by Duncan-Kemp (1933). In contrast, Sporn (1955) recorded thorny devils to consume 20 to 30 ants min^{-1} , with a meal lasting about 1 to $1\frac{1}{2}$ hours i.e. about 1875 ants per meal. We have observed a wide range of feeding rates in the field, from <1 to $>10 \text{ ants min}^{-1}$. Pianka & Pianka (1970) observed the stomachs of thorny devils to contain about 1 to 2 cm^3 (but up to 5 cm^3) of ants; typically there were about 2500 very small *Iridomyrmex*. It appears that the feeding rate, number of ants consumed per meal, length of meals, and number of meals per day might vary considerably, depending on factors such as ambient temperature, the size of the ants, and their abundance, and be higher for animals in captivity.

There were considerable differences among various species of ants in their water, energy, sodium and potassium contents. The *Iridomyrmex* 2 and *Crematogaster*

species which the thorny devils consumed were not unusual in either water, energy, sodium or potassium contents, and we suggest that the species of ants which thorny devils consume are determined more by the size, abundance and behaviour of the ants than any nutritional aspect.

Thorny devils move about 80 m day⁻¹ (spool measurements), which is fairly similar to a distance of about 50 m day⁻¹ determined by point-to-point daily; this is probably because thorny devils appear to be fairly sedentary, and move in fairly straight lines rather than meander widely. Over a period of 7 to 14 days, the thorny devils appeared to remain generally in the same area, as the long-term average point-to-point movement was only about 20 m day⁻¹ (see also Fig 4). Thus, thorny devils appear to rely on a food supply in a relatively small area, and their diet would reflect the local availability of ants (*Iridomyrmex* or *Crematogaster* spp). However, a few thorny devils were observed to move quickly over considerable distances (> 300 m d⁻¹), often essentially in a straight line; this contrasting movement pattern might reflect movements of individuals during the breeding season, or dispersing sub-adults or males. Movement records for longer periods are scarce, but the limited recapture data indicate that some individuals are extremely sedentary, even over 6 months to 3 years, whereas others had moved a kilometre or more after 6 months to 4 years.

Thorny devils were found to be active in the field over a wide range of body temperatures, as has been reported previously (Pianka & Pianka 1970; Pianka 1986). The mean of all T_b data recorded in this study was 28.3 °C ($\pm$ sd 6.6; $n=93$), which is slightly lower than that reported by Pianka (1986) of 32.6 ($\pm$ sd 4.1; $n=190$), at a slightly higher mean T_a of 27.1 °C ($\pm$ sd 5.2). The lower T_b 's and T_a 's reported here probably reflect the considerable data obtained for thorny devils located by spooling or radiotracking when inactive e.g. at night, and during cold and rainy conditions. The linear regression relationship of $T_b = 4.6 + 0.93 T_a$ was considerably different from that reported by Pianka (1986) of $T_b = 18.1 + 0.54 T_a$, and the regressions for $T_b < 32.5$ and $T_b > 32.5$ °C had a higher and lower slope, respectively, consistent with a non-linear relationship between T_b and T_a . Thorny devils are clearly not precise thermoregulators, and are not apparently restricted by T_b in being active, or feeding. In fact, one thorny devil was observed feeding in the rain, at a T_b and T_a of 16.5 °C! At extremely high T_a , thorny devils were seen to seek shelter in burrows, a behaviour not commonly observed otherwise.

Energetics of myrmecophagy

Thorny devils and other animals that specialise on eating ants (or termites) have a spatially clumped, but locally abundant prey. Their feeding strategy is usually an initial widely-foraging search and then a sit-and-wait feeding bout. This undoubtedly has marked implications for aspects of their ecology e.g. anti-predator strategies including crypsis and defensive spines, slow movements, thermolability, extended activity period, and a stout body with a large stomach (Pianka & Pianka 1970; Pianka 1986). In addition, a highly specialised diet of ants (or termites) potentially has important digestive and nutritional implications, and determines water,

energy and ion balance. The range of water content for the various ant species (40-80%; Table 1) is similar to that reported for other ants (75-77% for *Iridomyrmex* sp; 64% for 'desert ants'; Bradshaw & Shoemaker 1967; Minnich & Shoemaker 1972), and termites and other insects (generally 50-80%; Redford & Dorea 1984). There are few values for the energy content of ants, but our values, which range from 20 to 40 kJ g_{dry mass}⁻¹ (Table 1), are typical for most biological samples (e.g. d'Oleire-Oltmanns 1977), including termites (32 kJ g_{dry mass}⁻¹; Phelps *et al.* 1975). Hubert *et al.* (1981) reported a value of 17.3 kJ g_{wet mass}⁻¹, and 16.7 kJ g_{wet mass}⁻¹ for termites; values determined here for ants range from 5 to 15 kJ g_{wet mass}⁻¹. The sodium and potassium contents of the ants varied from about 50 to 250 $\mu\text{mol g}_{\text{dry mass}}^{-1}$, and the [sodium+potassium] content from about 100 to 500 $\mu\text{mol g}_{\text{dry mass}}^{-1}$. These values are similar to those reported for desert ants of 140 $\mu\text{mol Na}^+ \text{g}^{-1}$ and 142 $\mu\text{mol K}^+ \text{g}^{-1}$ by Minnich & Shoemaker (1972), but are considerably lower than the values of 670 and 860 $\mu\text{mol g}^{-1}$ reported by Bradshaw & Shoemaker (1967) for *Iridomyrmex* sp consumed by the dragon *Ctenophorus ornatus*. The ash content of our ant species would be at least 1 to 2.5%, calculated from a composition of 750 $\mu\text{mol g}_{\text{dry weight}}^{-1}$ of $\text{Na}^+ + \text{K}^+ + \text{Cl}^-$. The ash content of termites varies from <6 to >60%, generally being higher in workers than soldiers, and higher in some species that consume soil rather than wood (Redford & Dorea 1984). Unfortunately, we were unable to determine the ash content for the ants which we studied, but presumably they are more like that of soldiers of wood-consuming species (6-10%) than workers of some geophagous species (>60%). The nitrogen content of termites is generally about 1 to 10% of dry weight (Redford & Dorea 1984).

It is widely recognised that the digestion of ants and termites is difficult, in part due to their high chitin content (Pianka & Pianka 1970; Redford & Dorea 1984; Pianka 1986). The chitin content of termites varies from 5.1% to 16.5% (Tihon 1946; Hubert *et al.* 1981), and ants are even more sclerotised than termites (Redford & Dorea 1984). The high ash content, particularly of soil-consuming worker termites, would also decrease the digestibility and energy content. Nevertheless, we are unaware of any previous studies of the digestibility of ants or termites by myrmecophages, whether amphibian, reptilian, avian or mammalian. Our laboratory feeding trials with thorny devils, although only partly successful because none of the lizards consumed sufficient food to maintain a stable body mass, nevertheless indicate a low digestibility for ants. We estimate a metabolisable assimilation efficiency of about 59%, which is considerably less than that observed for lizards eating lightly-sclerotized insects (70-89% for mealworms and 70-90% for crickets), but is similar to that measured for heavily-sclerotized adult *Tenebrio molitor* (see Harwood 1979). Bell (1990) has estimated the dry matter assimilation of a "generalised" insect to be 78%, and the metabolisable energy assimilation to be 71%, assuming a total chitin content of 12.8% of dry mass, and excretion of nitrogenous wastes and urate. Ants presumably are more sclerotised and have a higher chitin content than a "generalised" insect, and the metabolisable energy assimilation of 59% for thorny devils is expected to be lower than for a "generalised" insect.

Field Turnovers

Our studies indirectly enable the estimation of the field energy requirements of free-living thorny devils, and indicate the approximate values for water, energy, sodium and potassium turnover for free-ranging lizards (Table 2). If we accept a feeding rate of about 1500 ants per day, each weighing 0.5 mg wet weight and 0.2 mg dry weight, with an energy content of 30 kJ g_{dry mass}⁻¹ and a metabolisable energy assimilation of 60%, then the calculated field metabolic rate is 5.4 kJ day⁻¹. This is considerably more than the predicted field metabolic rate of 3.4 kJ day⁻¹ for a 35g iguanid lizard (Nagy 1982a) and the actual field metabolic rate of 2.8 kJ d⁻¹ (Withers & Bradshaw 1995; Table 2). This discrepancy could be due to our over-estimating the feeding rate of thorny devils, the energy content of their food, or the digestibility of their food. The energy content of ants determined here is similar to expected values, and the metabolisable energy assimilation of 59% does not seem unreasonably low (see above), and so the assumption of a food intake of 1500 ants d⁻¹ is the most probable error. A feeding rate of 750 ants d⁻¹ yields the observed field energy turnover rate.

The feeding rate assumed above of 1500 ants day⁻¹ would confer a field water turnover rate (ignoring metabolic water production) of 0.45 ml day⁻¹, which is considerably lower than that predicted for a 30g semi-arid/arid lizard (0.84 ml day⁻¹; Nagy 1982b) but greater than the measured field water turnover rate of 0.30 ml d⁻¹ (Withers & Bradshaw 1995; Table 2). Accounting for metabolic water production (estimated as 0.03 ml kJ⁻¹; Withers 1992) increases the calculated field water turnover rate to 0.61 ml day⁻¹. A feeding rate of 750 ants d⁻¹ yields the observed field water turnover rate.

We can also estimate the field sodium and potassium turnover rates for thorny devils. If the sodium and

potassium contents of the ants are 180 and 240 µmol g_{dry mass}⁻¹ respectively, then the calculated turnover rates would be 54 µmol Na⁺ day⁻¹ and 72 µmol K⁺ day⁻¹ (if all dietary sodium and potassium were assimilated into the body pool). Surprisingly, this sodium turnover is less than that measured of 83 µmol d⁻¹, despite our having apparently overestimated the feeding rate. Sodium turnover has also been measured for other free-ranging lizards in order to estimate feeding rate. The field sodium turnover rate was about 1.0 to 1.2 µmol kg⁻¹ d⁻¹ for *Lacerta viridis* (Bradshaw *et al.* 1987), and 1.2 to 2.2 µmol kg⁻¹ d⁻¹ for *Ctenophorus (Amphibolurus) nuchalis* (Bradshaw *et al.* 1991). These values are similar to the calculated value of 0.8 (750 ants d⁻¹) to 1.5 (1500 ants d⁻¹) µmol kg⁻¹ d⁻¹ for thorny devils. We are unaware of any studies which have determined the field potassium turnover rate.

Although we were unable to determine the actual field water, energy and ion turnovers of thorny devils in this study, our results predict ratios of field turnover rates (Table 2). The ratio of field water turnover (WTR) to energy turnover (FMR) calculated for thorny devils is 0.11 ml kJ⁻¹ (0.61÷5.4). This ratio depends on the energy and water content of the diet, and its metabolisable energy assimilation (we assume that dietary water is 100% equilibrated with the lizard's body water pool), but not the absolute level of food consumption; it also assumes that the lizards are not able to drink in the field. Measurement of the ratio of WTR/FMR for thorny devils in the field as 0.11 ml kJ⁻¹ (Withers & Bradshaw 1995) suggests that we have correctly estimated the energy and water content of the diet, and its metabolisable energy assimilation, and that the thorny devils did not drink during the field study, although they clearly drink rain water and possibly dew when available (e.g. Bentley & Blumer 1962; Gans *et al.* 1982; Withers 1993; Sherbrooke 1993). The predicted ratio of WTR/FMR for a 30g semi-arid lizard is 0.25 (0.84÷3.4), suggesting that these "predicted" semi-arid lizards were drinking water.

Table 2

Field water, energy, sodium and potassium turnover rates, and ratios of rates, calculated for thorny devils from their diet, assuming a daily consumption of 1500 ants (wet mass 0.5 mg, dry weight 0.2 mg, 30 kJ g_{dry mass}⁻¹, 180 µmol Na⁺ g_{dry mass}⁻¹, and 240 µmol K⁺ g_{dry mass}⁻¹, compared with the allometrically-predicted values (for a 35 g lizard) and observed field values.

	Calculated from Diet	Predicted ¹	Measured ²
Field Turnover Rates			
WTR (ml d ⁻¹)	0.61	0.84	0.30
FMR (kJ d ⁻¹)	5.4	3.4	2.8
NaTR (µmol d ⁻¹)	54	≈60	83
KTR (µmol d ⁻¹)	72	-	-
Turnover Rate Ratios			
WTR/FMR (ml kJ ⁻¹)	0.11	0.25	0.11
NaTR/WTR (µmol ml ⁻¹)	89	≈71	277
KTR/WTR (µmol ml ⁻¹)	118	-	-
NaTR/FMR (µmol kJ ⁻¹)	10	≈18	30.2
KTR/FMR (µmol kJ ⁻¹)	13	-	-
NaTR/KTR	1.3	-	-

¹Nagy (1982a,b); Bradshaw *et al.* (1987, 1991)

²Withers & Bradshaw (1995; data for trip 4)

Acknowledgements: We are grateful to our numerous colleagues and students who assisted with these often arduous field studies of thorny devils. We sincerely thank Dr Jonathon Majer for identification of the various ants and John Dell for identification of the currant bush. We also thank Iain McLeod for assistance with ion analyses. All aspects of the study were undertaken with approval of the University of Western Australia Animal Welfare Committee and Radiation Protection Committee, the WA State Radiological Council, and the WA Department of Conservation and Land Management. A Roberts provided the photograph of the thorny devil.

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New records and further description of *Macrothrix hardingi* Petkovski (Cladocera) from granite pools in Western Australia

N N Smirnov¹ & I A E Bayly²

¹Institute for Animal Evolutionary Morphology and Ecology, Russian Academy of Sciences, Leninsky Prospekt 33, Moscow 117071, Russia

²Department of Ecology and Evolutionary Biology, Monash University, Clayton VIC 3168

Manuscript received June 1994; accepted September 1994

Abstract

New geographic records, taxonomic data and descriptive figures are presented for a cladoceran, *Macrothrix hardingi* Petkovski, which is recorded here from 8 new localities, all of which are shallow pools on granite rocks in Western Australia. This cladoceran species, which shows some similarities to *M. longiseta* Smirnov, is characterized *inter alia* by its dark black coloration and distinct occipital notch in the region of the head pore.

Introduction

Extensive collections of invertebrates from temporary pools on granite inselbergs in southern Western Australia have been made by one of us (IAEB) during the winters of 1977, 1990, 1992 and 1993. Some results from these samplings have already been published (Bayly 1982; Frey 1991), but most of it remains unpublished. Despite this, it is already clear that these small ephemeral aquatic habitats harbour a rich fauna (over 80 different metazoan taxa have thus far been recognised) with several species endemic to Western Australia. Frey (1991), for example, described a new genus of chydorid cladoceran (*Plurispina*) containing two species, both presently endemic to Western Australia, from the 1977 collections. Bayly (1992), in a paper dealing with some general aspects of granite rock-pools in Western Australia, listed several additional taxa including the cladoceran *Daphnia jollyi* Petkovski, that are known only from these distinctive habitats. The cladoceran, *Macrothrix hardingi*, which was originally described by Petkovski (1973) from two localities near Merredin, should now be added to this list of species from granite rock-pools. Collections made in 1990 and 1993 contained an abundance of this conspicuous, black cladoceran.

The cladoceran genus *Macrothrix* is well represented in Australia; there were 17 Australian species (including *M. hardingi*) out of a total generic complement of 34 species in a recent world review of the Macrothricidae (Smirnov 1992). Although *Macrothrix hardingi* was well figured by Petkovski (1973), this original description is not readily accessible to Australian workers. Consequently several new figures, including some of the features not included by Petkovski, are presented below.

Distribution and Taxonomy

Macrothrix hardingi Petkovski

(Figs 1-12)

Specimens examined

Specimens were examined from the following localities in Western Australia. Pool on south-west corner of

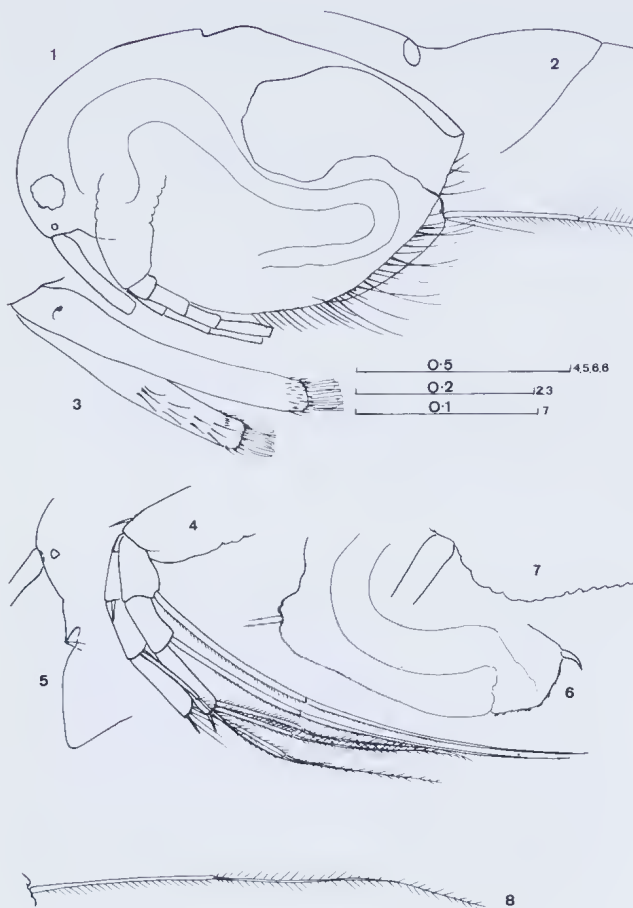
Elachbutting Rock; 30°36'S, 118°37'E; 15.viii.1990; 49 females. Pool on Sanford Rocks; 31°14'S, 118°46'E; 15.viii.1990; 9 females. Pool at southern edge of Mount Bailey [or Bayly]; 31°47'S, 119°07'E; 19.vi.1993; numerous females. Pool close to summit of Mount Bailey [or Bayly]; 31°47'S, 119°07'E; 19.vi.1993; numerous females. Pool near base of Geeraning Rock; 30°32'S, 118°36'E; 20.vi.1993; numerous females. Pool just below summit of Baladjie Rock; 30°57'S, 118°52'E; 22.vi.1993; numerous females. Pool on Chiddarcooping Hill; 30°54'S, 118°41'E; 22.vi.1993; numerous females. Pool at western end of Weowanie Rock; 31°08'S, 119°45'E; 23.vi.1993; numerous females.

Designation of neotype

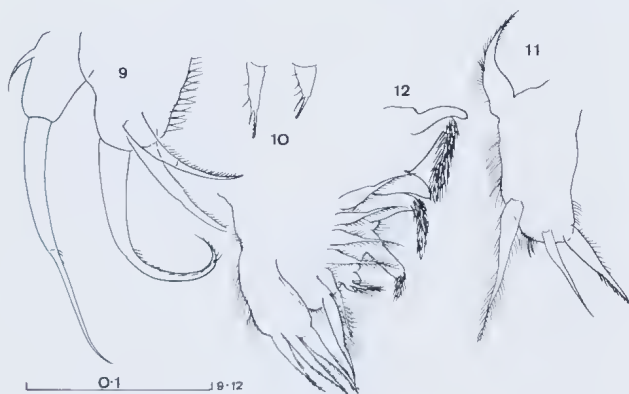
Since it has been established that there is now no original type material of *M. hardingi*, a neotype (female) has been deposited in the Australian Museum (Sydney) [Registered number P42691]. Reference slides have also been deposited in the Zoological Museum of Moscow University [Registered numbers 3672-3679.]

Description of female

Body outline oval in lateral view (Fig 1), with a distinct dorso-posterior angle. Dorsal outline arched, with occipital notch in region of head pore (Fig 2), slight hump posterior to occipital notch. Antennules (AI, Fig 3) rod-like, with groups of setae on distal part, with short sensory papillae. Antennae (AII, Fig 4) with setae 0-0-1-3/1-1-3, spines 0-1-0-1/0-0-1, spines much shorter than length of segments, largest seta of AII (proximal seta of 3-segmented branch) with very short unilateral setules along entire length. Labral lamella (Fig 5) short, cuneiform, with blunt apex. Postabdomen (Figs 6, 7) with minute setules on anal margin, preanal margin bare, with weak serrations. Setae natatoriae (Fig 8) with very long distal segments (1.5 times as long as proximal segments); total length of the setae natatoriae 0.75 times that of body length. Inner distal lobe of thoracic limb I (Fig 9) with 3 setae of different length, bearing unilateral short setules; Fryer's forks present on thoracic limb I (Fig 10). Exopodites of thoracic limbs III (Fig 11) with 4 setae. Exopodites of thoracic limbs IV (Fig 12) with 3 setae. Up to 10 parthenogenetic eggs in brood pouch. Length ca 1.5 mm. [The male is unknown.]



Figures 1-8. *Macrothrix hardingi* Petkovski, drawn from material collected from Sanford Rocks, Western Australia. Scale bars in mm. 1, left lateral aspect of whole animal; 2, magnification of dorsal occipital notch and head pore; 3, AI (antennules); 4, AII (antennae); 5, labrum; 6, postabdomen; 7, proximal portion of postabdomen; 8, seta natatoria.



Figures 9-12. *Macrothrix hardingi* Petkovski. 9, outer distal lobe and inner distal lobes of thoracic limb I; 10, Fryer's forks of thoracic limb I; 11, exopodite of thoracic limb III; 12, thoracic limb IV.

Differential diagnosis

Macrothrix hardingi, in addition to its black colour, differs from other *Macrothrix* species (see Smirnov 1992) in AI not dilating distally and in having no strong spines. The largest antennal seta has short setules on one side only. The dorsal outline has a characteristic depression in the region of head pore. The postabdomen is not bilobed and has very short setules. *Macrothrix hardingi* is somewhat similar to *M. longiseta* Smirnov, differing from it in the absence of long setules along the distal segment of the outer distal lobe of thoracic limb I and in the black colouration.

It is important to note that Smirnov & Timms (1983) separated *Echinisca* Liévin from *Macrothrix* Baird on the key feature that the antennules are dilated distally in the latter but not in the former. On this basis, *hardingi* would have to be referred to *Echinisca*. However, Smirnov (1992) synonymised *Echinisca* with *Macrothrix*.

Ecology

Macrothrix hardingi lives in pools that are commonly less than 10cm deep in the middle, and is often abundant in the very shallow (less than 1cm deep) water at the extreme edges of the pools. It is very conspicuous to the naked eye by virtue of its jet-black colour against the light-coloured granite. In this respect it resembles *Daphnia jollyi*, another cladoceran that is restricted to granite rock-pools in Western Australia. The pools inhabited by *Macrothrix hardingi* and *Daphnia jollyi* contain very clear water and it is physically impossible for these species to avoid strong light because of the extreme shallowness of the pools. It is likely that the heavy black pigmentation is photo-protective, preventing damage from potentially injurious ultraviolet light. The calanoid copepod, *Boeckella opaquua* Fairbridge, another species confined to the same type of habitat as these two cladocerans, is also invariably strongly pigmented but is bright red from the accumulation of carotenoids.

Acknowledgments: This study was partly supported by a grant of the G Soros International Science Foundation to one of us (NNS).

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Preliminary observations on termite diversity in native *Banksia* woodland and exotic pine *Pinus pinaster* plantations

M Abensperg-Traun¹ & D H Perry²

¹ CSIRO, Division of Wildlife and Ecology, LMB No 4, Midland WA 6056

² 26 Egham Road, Victoria Park WA 6100

Manuscript received September 1994, accepted February 1995

Abstract

Preliminary observations on termite diversity recorded 16 termite species from 10 genera for native *Banksia* woodland at Gnangara on the Swan Coastal Plain and 7 species from 5 genera for adjacent areas of 40 - 70 year-old exotic maritime pine *Pinus pinaster* plantations. Only 3 species were recorded eating pine; the remaining 4 species in pine plantations survived by foraging on remnant stumps, logs and roots of *Eucalyptus* only. We hypothesize that low termite diversity in pine may in part be due to replacement of palatable native woody plants with unpalatable exotic pine and changes in soil microclimatic conditions. Following plantation establishment, reinvasion by termites appears not to occur as readily as it does by other soil and litter arthropods.

Introduction

The diet of termites consists principally of cellulose obtained from living, dead but sound, or decomposed vegetation, humus or soil, or various combinations of the above (Wood 1978). Although the wood of many species of plant may be eaten, there is generally considerable partitioning of the available food resource within any particular habitat. Species of *Coptotermes* and *Heterotermes*, for instance, are able to eat relatively undecayed wood with high levels of plant chemical defences, while others such as species of *Amitermes* eat more decayed wood, including humus (Wood 1978; Miller 1991). Certain native and exotic tree species may be preferred or avoided by the termites (French *et al.* 1981; Postle & Abbott 1991; Abensperg-Traun 1993; Abensperg-Traun *et al.* 1993). In Australia, the exotic pines *Pinus pinaster* and *P. radiata* have not been readily accepted by many termite species; notable exceptions are species of *Coptotermes* and *Heterotermes*, and the tropical *Mastotermes darwiniensis* (e.g. Gay 1957; Greaves 1959; Spragg & Paton 1980; Abensperg-Traun 1993). Replacement of native vegetation with pine plantations may thus be associated with a marked decline in termite diversity. No previous Australian studies have compared termite communities in native woodland with communities inhabiting pine plantations. The present study reports preliminary results of surveys on termite diversity in native *Banksia* woodland on the Bassendean sands of the Swan Coastal Plain, and on adjacent stands of 40 - 70 year-old maritime pine.

Methods

Study area

The study was conducted at the Gnangara Pine Plantation (31°45'S, 115°48'E), about 20 km north of Perth,

Western Australia, where pine plantations abutt onto native *Banksia* woodland. The soils are Bassendean sands, described in detail by McArthur & Bettenay (1960). The area has a mediterranean climate with cool wet winters and hot dry summers, with a mean annual rainfall of 866 mm (Bureau of Meteorology, Perth).

Native vegetation on the Bassendean sands at Gnangara is mostly open *Banksia* woodland. *Melaleuca raphiophylla* (paperbark), *Nuytsia floribunda* (christmas tree), and species of *Allocasuarina* (she-oak) are also common. Eucalypts such as *Eucalyptus calophylla* (marri), *E. marginata* (jarrah), *E. tottiana* (coastal blackbutt) and *E. rudis* (flooded gum) are largely restricted to the swales between coastal dune systems. The shrubby understorey is diverse and consists predominantly of species of *Acacia*, *Xanthorrhoea*, *Hakea*, *Jacksonia*, *Melaleuca* and *Adenanthos* (Havel 1976; Heddle 1980).

For the establishment of pine plantations at Gnangara in the late 1920's and early 1930's, all banksias and eucalypts were clear-felled. The area was then burnt. Only logs of large trees survived the burn, and these were left on the ground. The area was then ploughed and pine seedlings were planted. Controlled burns in pine plantations at Gnangara are part of management strategy and usually follow thinning operations (C Sanders, CALM, *pers comm*).

Termite sampling

Termites were sampled opportunistically, using a spade and axe, by D H Perry from 1953 to 1966. The collections were made over an area of about 500 ha of *Banksia* woodland, and about 200 ha of two approximately 30 year-old pine stands (Wetherell Block). The pine stands replaced a *Banksia* woodland containing large eucalypts, and remnants of these were still present at sampling time. Termites were sampled in the soil, mounds (termitaria) and timber, and a list of all collected species was recorded. The pine plantations origi-

nally sampled for termites by D H Perry were again sampled in August and November 1994, allocating a total of approximately 4 man-hours to each of two study areas. Approximately 2 ha were sampled in each area. Specimens were identified to species following Perry *et al.* (1985). *Banksia* woodland was not sampled in 1994. We therefore assume that termite diversity in the *Banksia* woodland at the present time resembles that when sampled about 35 years ago, and that the early surveys remain a valid control to the 1994 data.

The first pine stand (Area 1; Compartment 15) was planted in 1930 and contained no large eucalypt trees prior to plantation establishment. It was clear-felled and replanted in 1962 following a fire. It had not been 'thinned' when sampled in 1994, with a dense stand of 15 - 20 m tall pines at 2 - 3 m intervals. Canopy cover was close to 100 %, and a 15 to 20 cm deep layer of pine needles covered the soil surface suggesting that the stand had not been burnt since it was planted. There was no understorey of native (or exotic) plants with the exception of a small number of *M. raphiophylla*. No remnants of *Banksia* stumps or roots were located, so termite sampling was restricted to the soil, and to standing and fallen dead pine.

The immediately adjacent pine stand (Area 2; Compartment 4) was planted in 1927. It supported *Banksia* as well as large jarrah and marri trees prior to the establishment of pines, and carried its first crop of approximately 30 m tall pines when sampled in 1994. The stand had been thinned to a density of approximately one tree at about 15 m intervals, giving a canopy cover of < 25 %. Although both areas had been under pine for over 60 years, they differed markedly as habitat for termites. In contrast to Area 1, Area 2 contained numerous remnants of eucalypt logs and stumps, and also regenerating balga (*Xanthorrhoea preissii*), paperbark (*M. raphiophylla*), jarrah (*E. marginata*) and marri (*E. calophylla*), which might provide foraging and nesting sites for termites. Low tree density and pine needle cover would facilitate higher levels of penetration of sun light, more closely resembling pre-plantation conditions.

Results and Discussion

The survey of *Banksia* woodland, about 35 years ago, identified 16 termite species from 10 genera (Table 1). Sampling within adjacent pine plantations identified only four species, three of which survived on a diet of pine (*Coptotermes aciuciformis raffrayi*, *C. michaelsoni* and *H. platycephalus*); *Amitermes modicus* was recorded foraging on jarrah logs only.

In 1994, we recorded six species of termite in pine plantations, bringing the total termite diversity for pine plantations to 7 species (Table 1). In the unthinned stand, Area 1 which lacked remnants of eucalypt logs and stumps, we recorded only *Coptotermes michaelsoni*. In the open, older stand, Area 2, we recorded two species of *Coptotermes* and one species of *Heterotermes* eating pine. *Hesperotermes infrequens*, *Amitermes conformis* and *Xylochomitermes occidialis* were recorded on remnant jarrah logs and stumps; *A. conformis* was also sampled within mounds of *C. a. raffrayi*. Stumps and fallen timber of *M. raphiophylla* did not support any termites. No

Table 1

Termite species recorded from native *Banksia* woodland at Gngangara on the Bassendean sands of the Swan Coastal Plain, and species recorded where *Banksia* had been removed and replaced with maritime pine (*Pinus pinaster*).

Termite species	<i>Banksia</i> woodland	Pine plantation		
	Sampled 1953 to 1966	Sampled 1953 to 1966	Sampled in 1994 Without <i>Eucalyptus</i>	With <i>Eucalyptus</i>
Kalotermitidae				
<i>Kalotermes hilli</i>	+			
Rhinotermitidae				
<i>Coptotermes a. raffrayi</i>	+	+		+
<i>Coptotermes michaelsoni</i>	+	+	+	+
<i>Heterotermes occidius</i>	+			
<i>Heterotermes platycephalus</i>	+	+		+
Termitidae				
<i>Amitermes conformis</i>	+			+
<i>Amitermes heteroguthus</i>	+			
<i>Amitermes modicus</i>	+	+		
<i>Amitermes sp.</i>	+			
<i>Hesperotermes infrequens</i>	+			+
<i>Microcerotermes newmani</i>	+			
<i>Nasutitermes exitiosus</i>	+			
<i>Occasitermes occasus</i>	+			
<i>Paracaprithermes kraepelinii</i>	+			
<i>Xylochomitermes occidialis</i>	+			+
<i>Xylochomitermes tomentosus</i>	+			
Total number of species	16	4	1	6

termites were found inhabiting the top layer of the soil, despite the availability of a rich humus layer. The genera recorded in *Banksia* woodland but not in pine plantations are *Kalotermes*, *Microcerotermes*, *Nasutitermes*, *Occasitermes* and *Paracaprithermes* (Table 1).

Termite diversity in pine plantations may have been low compared to *Banksia* woodland because the area sampled for termites, and sampling effort, was greater for *Banksia* than for pine areas. However, we hypothesize that two factors may have contributed to the lower termite diversity of pine plantations; (1) replacement of palatable native woody plants with exotic, unpalatable species, and (2) modification of soil microclimatic conditions.

Chemical composition of the timber, and hence its palatability, is often of critical importance to foraging termites (Wood 1978; Wood & Johnson 1986). For example, *Nasutitermes exitiosus* does not appear to eat pine and this may be because essential oils in the timber contain chemicals which are an important constituent of the termites' alarm pheromone (Moore 1969). Consistent with our observations, termite attacks on pine baits in the central wheatbelt of Western Australia were also restricted to *Coptotermes* (1 species) and *Heterotermes* (1 species) despite the presence of a species-rich community of wood-eating termites (Abensperg-Traun 1993).

Studies in eastern Australia show a progressive decline of *Nasutitermes exitiosus* colonies under pine plantations. This has been attributed to lower soil temperatures due to excessive shade rather than lack of food because the durable logs and stumps of eucalypt timber

remained for many years (Ratcliffe *et al.* 1952; Gay 1957; Lee & Wood 1971). Our observations are consistent with these other studies.

Several studies have shown that the diversity of other soil and litter arthropods is markedly lower in pine compared to relatively undisturbed native vegetation on similar soils (Springett 1971, 1976; Majer 1978, 1985; Rossbach & Majer 1983). Some of these studies (*e.g.* Springett 1976) also indicate that with increasing age of the plantation, arthropod diversity also increases. Successful reinvasion by other arthropods may be influenced by a progressive decline in canopy and pine needle cover through logging and fire. Our observations suggest that the rate of reinvasion by termites may be slower compared to many other arthropods, and that the return of native trees for food may be an important factor influencing reinvasion by termites.

The observations reported here are clearly preliminary. However, given that about 70 000 ha are under pine plantations in south-west Western Australia (Abbott 1993), an experimental study into the long-term effects of pine plantations on termite diversity is warranted.

Acknowledgements: We thank C Sanders (CALM) for permission to collect termites at Gnangara. I Abbott, D Ewart and G Smith commented constructively on the manuscript, for which we are grateful.

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- Abbott, I J** ORD December 1976
(b) Department of Conservation & Land Management, Australia 11 Drive, Crawley WA 6009 ph:442-0309 fax:386-6399
interests: ecology, forests, islands, soil biology, science policy
- Abensperg-Traun, M** ORD March 1991
(b) Division of Wildlife and Ecology, CSIRO, LMB No 4, Midland WA 6056 ph: 290-8132 fax: 290-8134
interests: ecology: invertebrates, myrmecophagy, conservation biology
- Ahmat, A L** ORD May 1970 Kalgoorlie WA
- Allen, A D** ORD July 1976 East Perth WA
- Arbuckle, D J F** ORD October 1983 Farramere, South Africa
- Armstrong, C J** ORD April 1991 Armadale WA
- Atkins, R P** ORD November 1976
(b) Waterways Commission, 216 St Georges Terrace, Perth WA 6000 ph: 327-9738 fax: 327-9770
(h) 21 Hartung Street, Mundaring WA 6073 ph: 295-2954
interests: management of waterways
- Atkinson, D M M** ORD July 1976 Claremont WA
- Atkinson, P R** ORD May 1970
(b) 28 Ruskin Street, Parnell Auckland New Zealand
ph: (09) 303-1893 fax: (09) 303-1612
- Backhouse, J** ORD July 1976
(b) Geological Survey of WA, 100 Plain Street, East Perth WA 6004 ph: 222-3159
interests: palaeontology, palynology, stratigraphy, geology, Palaeozoic and Mesozoic sedimentary rocks in WA
- Bailey, J M** ORD May 1988 Murdoch WA
- Baird, A M** HON July 1928 [1973] Peppermint Grove WA
- Baker, S K** ORD April 1987 Nedlands WA
- Balla, S A** ORD December 1992
(b) Environmental Management, Water Authority of WA, Leederville WA 6007 ph: 420-3242 fax: 420-3176
(h) 1 Wongan Avenue, Hilton WA 6163 ph: 335-5238
interests: ecology, wetlands
- Balme, B E** ORD November 1958 Claremont WA
- Balme, H E** HAS July 1980 Claremont WA
- Balme, J M** ORD July 1976 Armadale NSW
- Bamford, M J** ORD March 1988
(b) MJ & AR Bamford Consulting Ecologists, 23 Plover Way, Kingsley WA 6026 ph: 309-3671
interests: ecology, small vertebrates [frogs, reptiles, birds, mammals], fire, mine site rehabilitation
- Bannister, J L** ORD June 1967 Perth WA
- Barley, M E** ORD April 1987 Nedlands WA
- Bathgate, J A** ORD
(h) 14 Langer Street, East Victoria Park WA 6101
ph: 361-3416
interests: plant pathology, diseases of native plants
- Bayly, I A E** ORD March 1992
(b) Department of Ecology & Evolutionary Biology, Monash University, Clayton VIC 3168 ph: (03) 905-5667 fax: (03) 905-5613
E-mail: IAN.BAYLY@SCI.MONASH.EDU.AU
(h) 114 Belgrave-Hallam Road, Belgrave South VIC 3160
interests: limnology, animals, invertebrate zoology, ecology, WA granites
- Baynes, A** ORD August 1967 Perth WA
- Beard, J S P** HON June 1962 [1990] [Medallist 1983] Applecross WA
- Beggs, B J** ORD July 1971 Booragoon WA
- Bekle, H** ORD July 1982 Minora WA
- Bell, D T** ORD August 1977
(b) Botany Department, University of Western Australia, Nedlands WA 6907 ph: 380-215 fax: 380-1001
E-mail: dbell@uniwa.uwa.edu.au
(h) ph: 450-3569
interests: plants, ecology
- Bennett, E M** ORD September 1963 Gooseberry Hill WA
- Berry, P F** ORD July 1980 Perth WA
- Bevan, A W R** ORD Perth WA
- Birch, P V** ORD May 1987
(b) Perth Observatory, Walnut Road, Bickley WA 6076
ph: 293-8255 fax: 293-8138
E-mail: pvbirch@earwax.pd.uwa.edu.au
interests: astronomy
- Black, W R** ORD April 1987 Nedlands WA
- Blyth, J D** ORD April 1987 Wanneroo WA
- Boardman, W J** ORD December 1984 Salter Point WA
- Borowitzka, M A** ORD August 1986
(b) Biological & Environmental Sciences, Murdoch University, Murdoch WA 6150 ph: 360-2333 fax: 310-3505
E-mail: borowitz@possum.Murdoch.edu.au
interests: algae [biotechnology, primary production, toxins, sponge symbioses, blooms, ecology], coral reef, bioactive molecules, marine biology, seagrass epiphytes
- Bottomley, G A** ORD July 1971 Claremont WA
- Bougher, A R** ORD June 1987 Mount Hawthorn WA
- Bourgault du Coudray, P L** STU September 1991
(b) Division of Environmental Science, Murdoch University, Murdoch WA 6150 ph: 360-6396 fax: 310-4997
E-mail: bourgau@cuvax1.Murdoch.edu.au
(h) Lot 5296 Hudman Road, Boya WA 6056 ph: 299-8176
interests: soils [solute leaching, macropores, salinity control], salinity [solute leaching and movements, control], drylands
- Bowdler, S** ORD July 1983 Nedlands WA
- Bowers, C L** ORD June 1987 Kalamunda WA
- Bradley, J S** ORD October 1993 Murdoch WA
- Bradshaw, S D** ORD December 1965
(b) Zoology Department, University of Western Australia, Nedlands WA 6907 ph: 380-3769 fax: 380-1029
E-mail: bradshaw@uniwa.uwa.edu.au
(h) 156 Hensman Road, Subiaco WA 6008 ph: 381-5010
interests: comparative endocrinology, ecophysiology of desert animals, arid-zone, adaptation, philosophy of science, physiology
- Brearley, A** STU October 1993 Nedlands WA
- Bridge, P J** ORD March 1966
(b) Hesperian Press, 65 Oats Street, Carlisle WA 6101
ph: 362-5955 fax: 361-2333
(h) 61 Washington Street, Victoria Park WA 6100
interests: mineralogy, history
- Bridgewater, P** ORD July 1976 Canberra ACT
- Briggs, I M** ORD December 1983
(b) Agricultural and Resource Economics, Faculty of Agriculture, University of Western Australia, Nedlands WA 6907 ph: 380-2105 fax: 380-1098
E-mail: ibriggs@uniwa.uwa.edu.au
(h) 37 Meriwa Street, Nedlands WA 6009
interests: natural resource management, water resources, regional resource planning
- Brooker, M G** ORD April 1987 Midland WA
- Brown, R G** ORD April 1987
(b) Geology and Geophysics Department, University of Western Australia, Nedlands WA 6907 ph: 380-2679 fax: 380-1037 E-mail: rbrown@uniwa.uwa.edu.au
(h) 2 Rowan Place, Woodlands WA 6018 ph: 446-2171
interests: geology, sedimentology, quaternary history

- Bunn, E R ORD December 1985 West Perth WA
 Bunn, S E ORD October 1985 Nathan QLD
 Burbidge, A A ORD July 1983 Wanneroo WA
 Burbidge, A H ORD June 1978
 (b) WA Wildlife Research Centre, Department of Conservation & Land Management, PO Box 51, Wanneroo WA 6065 ph: 405-5100 fax: 306-1641
 interests: biogeography, birds, conservation, threatened birds
- Burman, R R ORD March 1988 Nedlands WA
 Burne, R V ORD May 1991
 (b) Australian Geological Survey Organisation, PO Box 378, Canberra ACT 2601 ph: (06) 249-9291
 fax: (06) 249-9970 E-mail: rburne@agso.gov.au
 interests: coastal geoscience, stromatolites, microbialites, coastal geoscience
- Burrows, N D ORD March 1994
 (b) Department of Conservation and Land Management, 50 Hayman Road, Como WA 6152 ph: 334-0300
 fax: 334-0327
 (h) 21 Sandra Way, Rossmoyne WA 6148 ph: 354-2637
 interests: forestry [science and management], fire [management, behaviour, ecology], ecology, arid-zones
- Butler, R J T ORD August 1965 South Guildford WA
 Calver, M C ORD July 1989 Bateman WA
 Cannon, J R ORD April 1987
 (b) Department of Chemistry, University of Western Australia, Nedlands WA 6907 ph: 380-3152 fax: 380-1005
 interests: chemistry, natural products, development in South East Asia
- Carey, S W LIF July 1933 Dynnyrne TAS
 Carstairs, S ORD Como WA
 Chalmer, P N ORD May 1981 Mount Barker WA
 Christensen, P E S ORD July 1978 Balingup WA
 Churchill, D M ORD May 1956 Apollo Bay VIC
 Cleverly, W H HON July 1938 [1982] Kalgoorlie WA
 Coates, D ORD Como WA
 Cockbain, A E ORD July 1976 South Perth WA
 Coleman, P J ORD October 1963 Nedlands WA
 Collins, M T ORD March 1990 Melville WA
 Collins P ORD June 1987 Woodlands WA
 Colquhoun, I J ORD February 1983 Applecross WA
 Conacher, A J ORD October 1972
 (b) Geography Department, University of Western Australia, Nedlands WA 6907 ph: 380-2705
 fax: 380-1054
 interests: soil, soil/slope relationships, rural environment, land degradation and management
- Congdon, R A ORD July 1975
 (b) Department of Botany and Tropical Agriculture, James Cook University, Townsville QLD 4814 ph: (077) 81-4731
 fax: (077) 25-1570 E-mail: robert.congdon@jcu.edu.au
 interests: plants [ecology, productivity, nutrient cycling, rainforest, wetlands], ecology, agroforestry, forestry
- Connell, S W ORD March 1988 Kallaroo WA
 Considine, J A ORD September 1987
 (b) Plant Sciences, Faculty of Agriculture, University of Western Australia, Nedlands WA 6907 ph: 380-1783
 fax: 380-1108 E-mail: consid@uniwa.uwa.edu.au
 (h) 201 Millbank Drive, Bidaminna WA 6503
 ph: (096) 553009 fax: (096) 553009
 interests: seeds [physiology, dormancy, germination], plants [development, productivity, improvement], floriculture, tropical fruit [growth, development]
- Cowling, W A ORD July 1983
 (b) Department of Agriculture, Baron-Hay Court, South Perth WA 6151 ph: 368-3528 fax: 474-2840
 (h) 81 Arlington Avenue, South Perth WA 6151
 interests: plants, genetic resources
- Crawford, I M ORD November 1961
 (h) 5 Kirway Street, Floreat Park WA 6014 ph: 387-3019
 interests: archaeology, aboriginal studies
- Creed, K E ORD July 1987 Murdoch WA
 Cresswell, I D ORD July 1987 Belconnen ACT
 Crombie, D S ORD October 1985 Dwellingup WA
 Curry, S J HON December 1966 Swanbourne WA
- Davies, S J J ORD September 1977 Mount Helena WA
 Davis, C E S ORD March 1938 Floreat Park WA
 Davison, E M ORD April 1982
 (b) Department of Conservation and Land Management, Brain Street, Manjimup WA 6258 ph: (097) 71-1988
 fax: (097) 77-1183
 (h) 148 Bateman Road, Mt Pleasant WA 6153
 ph: 364-3816
 interests: plant pathology, mycology, forestry, botany
- Davy, R ORD December 1966
 (b) Geochemistry Section, Geological Survey of WA, 100 Plain Street, East Perth WA 6004 ph: 222-3153
 fax: 222-3622
 (h) 13-B Todd Avenue, Como WA 6152 ph: 367-3248
 interests: geology, exploration, geochemistry, economic geology, geochemistry
- De Laeter, J R ORD June 1972
 (b) School of Physical Sciences, Curtin University of Technology, GPO Box U1987, Perth WA 6000
 ph: 351-3045 fax: 351-3048
 (h) 4 The Parapet, Burrendah WA 6155 ph: 457-2578
 interests: astrophysics, science education, physics, mass spectrometry
- del Marco, A P ORD November 1992 North Perth WA
 Dell, B ORD June 1975 Murdoch WA
 Dickman, C R ORD April 1986 Sydney NSW
 Dixon, K W ORD June 1984
 (b) Kings Park and Botanic Gardens, Kings Park Road, West Perth WA 6005 ph: 480-3629 fax: 322-5064
 (h) 36 Branksome Gardens, City Beach WA 6015
 ph: 385-7969
 interests: plants [conservation, seed germination, micropropagation, germplasm storage, breeding], habitat restoration, taxonomy
- Dodd, J ORD April 1978
 (b) Department of Agriculture, Baron-Hay Court, South Perth WA 6151 ph: 368-3679 fax: 474-3814
 interests: weeds, biological control, plants, ecology, Rottnest Island, terrestrial vegetation, banksia woodland
- Dodds, F S ORD April 1972 Wembley WA
 Doupe, R G STU August 1993 West Perth WA
 Dyson, S E ORD October 1993 Mount Pleasant WA
 Edinger-Reeve, R ORD May 1988
 (b) Department of Employment, Education, Training, WA Area South Office, 13th Floor QV1, 250 St Georges Terrace Perth WA 6000 ph: 429-3609 fax: 429-3707
- Eliot, I G ORD August 1981 Nedlands WA
 Elkington, C R ORD September 1958 Kenwick WA
 Evans, C A ORD May 1990 Floreat WA
 Farrington, P ORD March 1981
 (b) Division of Water Resources, CSIRO, Private Bag, Wembley WA 6014 ph: 387-0395 fax: 387-8211 E-mail: Peter@Per.DWR.CSIRO.au
 (h) 4 Thomas Way, Karrinyup WA 6018 ph: 341-1055
 interests: plants, water use, salinity, agroforestry, hydrology, catchments, forestry, agroforestry
- Ferguson, W C ORD March 1978 St Kilda VIC
 Finucane, S J ORD
 (b) Dames and Moore, South Shore Centre, 85 The Esplanade, South Perth WA 6151 ph: 367-8055
 fax: 367-6780
 (h) 06/21 Angelo Street, South Perth WA 6151
 ph: 367-8949
 interests: ecology, arid zone biology, wetlands, environmental impact assessment and management
- Firman, J B ORD August 1988
 (h) 14 Giddens Court, North Lake WA 6163 ph: 331-2742
- Foulds, W ORD November 1981
 (h) 86 Lakelands Drive, Gnangara WA 6065 ph: 306-3354
 interests: plant ecology
- Fox, J E D LIF July 1975 Bentley WA
 Friend, G R ORD April 1987 Wanneroo WA
 Friend, J A ORD April 1987 Wanneroo WA
 Froend, R H ORD September 1988
 (b) Surface Water Branch, Water Authority of WA, P O Box 100, Leederville WA 6007 ph: 420-3118

- fax: 420-3176 E-mail: froend@essun1.Murdoch.edu.au
(h) 60 Harris Road, Bicton WA 6157 ph: 339-2804
interests: plants [ecology, aquatic, terrestrial, water relations], wetlands, ecology, management,
- Gardner, P E** ORD July 1992 North Fremantle WA
- Garnett, P J** ORD
(b) Edith Cowan University, Joondalup Drive, Joondalup WA 6027 ph: 405-5665 fax: 405-5717
E-mail: P.Garnett@cowan.edu.au
(h) 17 Radstock Street, Karrinyup WA 6018 ph: 447-7724
interests: environmental chemistry, chemistry, education, environment
- Gazey, P** STU November 1993 Maida Vale WA
- Geary, J K** ORD September 1943 Karrinyup WA
- Gentili, J** HON September 1993 [1993]
(b) Department of Geography, University of Western Australia, Nedlands WA 6907 ph: 380-2664
fax: 380-1054
(h) 65 Bruce Street, Nedlands WA 6009 ph: 386-2492
interests: climatology, biogeography, migrations
- George, A S** ORD June 1961
(b) 'Four Gables', 18 Barclay Road, Kardinya WA 6163
ph: 337-1655 fax: 337-9404
(h) as above
interests: plants, systematics of Australian flora, natural history, editing texts
- George, P R** ORD March 1987 Karrinyup WA
- Ghisalberti, E L** ORD April 1989 Nedlands WA
- Gibson, N** ORD April 1991 Wanneroo WA
- Gladstones, J S** ORD March 1957
(b) 27 Pandora Drive, City Beach WA 6015 ph: 385-9436
(h) as above
interests: agronomy, plant breeding, viticulture, ecology
- Glassford, D K** ORD December 1984 Bullcreek WA
- Glover, J J E** HON July 1956 [1982] Nedlands WA
- Goble-Garratt, D** ORD April 1989
(b) 117 Tower Street, West Leederville WA 6007
ph: 382-2383 fax: 382-2383
(h) as above
interests: natural science, resource utilisation, urban environments
- Gole, M J** ORD December 1984 Gooseberry Hill WA
- Gordon, D M** ORD December 1979
(b) LeProvost, Dames & Moore ph: 474-1933
fax: 368-2294
interests: ecology and physiology of aquatic plants, ecophysiology of mangroves, photosynthesis of marine and freshwater plants
- Gozzard, J R** ORD April 1989 East Perth WA
- Graham, J** ORD February 1973 Wembley WA
- Gray, N M** ORD April 1948
(h) 7/9 Sutherland Street, Cremorne NSW 2090
ph: (02) 908-4443
interests: engineering geology, geophysics, regional geology
- Grayling, P M** ORD October 1984 Fremantle WA
- Grieve, B J** HON July 1948 [1975] [Medallist 1979]
(b) P O Box 613, Nedlands WA 6009
(h) Unit 142, St Louis Estate Retirement Village, 3 Dean Street, Claremont WA 6010 ph: 384-4819
- Griffin, E A** ORD March 1978 Victoria Park WA
- Groves, D I** ORD March 1971 Nedlands WA
- Guppy, M** ORD
(b) Biochemistry Department, University of Western Australia, Nedlands WA 6907 ph: 380-3331
fax: 380-1148 E-mail: mguppy@uniwa.uwa.edu.au
interests: biochemistry, metabolism, metabolic depression
- Haig, D W** ORD October 1985 Nedlands WA
- Hall, G P** ORD June 1990 Como WA
- Hallam, S J** ORD June 1967
(h) 2 Pool Street, York WA 6302
interests: archaeology (Australia), prehistoric settlement, ecology
- Hallberg, J A** ORD August 1970 Neerabup WA
- Halse, S A** ORD April 1992 Wanneroo WA
- Hamilton, R** ORD March 1991 Como WA
- Hardy, G E St J** ORD April 1994 Murdoch WA
- Hare, R** ORD April 1950 San Lorenzo, Makati Metro Manila, Phillipines
- Harris, P G** ORD July 1976 Nedlands WA
- Hart, R P** ORD April 1982
(b) Hart, Simpson & Associates, 324 Onslow Road, Shenton Park WA 6008 ph: 388-3972 fax: 382-1395
(h) 21 Rankin Road, Shenton Park WA 6008 ph: 382-1086
interests: environmental impact assessment, ecology, wildlife, plants [disease, dieback], environmental management
- Harvey, M S** ORD March 1992
(b) Curator of Arachnology, WA Museum, Francis Street, Perth WA 6000 ph: 427-2737 fax: 328-8686
E-mail: harvey@muswa.dialix.oz.au
interests: arachnology, taxonomy [arachnids]
- Hatch, A B** HON July 1958 [1982] Murdoch WA
- Hatcher, B G** ORD April 1987
(b) CFRAMP-Resourcement Unit, Tyrell Street, Kingstown, St Vincent WEST INDIES ph: (809) 457-1904
fax: (809) 457-2414
(h) CFRAMP-Resource Assessment Unit, Tyrell Street, Kingstown WEST INDIES ph: (809) 456-9621
interests: benthic ecology, oceanography, conservation biology, fisheries, marine geology
- Hefter, G T** ORD September 1993 Murdoch WA
- Hesp, P A** ORD April 1992 Singapore
- Hilliard, R W** ORD October 1993
(b) LeProvost Dames & Moore, Level 5 South Shore Plaza, 85 The Esplanade, South Perth WA 6151 ph: 474-1933
fax: 367-6780
(h) Lot 8 Burton Road, Darlington WA 6070
interests: environmental impact assessment, environmental management [marine, coastal, riverine], monitoring studies
- Hillman, R M** ORD April 1987 Dalkeith WA
- Hnatiuk, R J** ORD July 1976 Cook ACT
- Hobbs, A A** ORD November 1992 Nedlands WA
- Hobbs, R J** ORD September 1984 Midland WA
- Hobbs, V J** ORD September 1984
(b) Mathematical and Physical Sciences, Murdoch University, Murdoch WA 6150 ph: 360-2817
- Hobday, J D** ORD March 1974 Mosman Park WA
- Hodgkin, E P** HON July 1946 [1975]
(h) 86 Adelma Road, Dalkeith WA 6009 ph: 386-7895
interests: ecology, estuaries
- Hodgson, E C** ORD July 1946 Dalglish WA
- Hopkins, E R** ORD November 1959 Manning WA
- Hopper, S D** ORD December 1976 West Perth WA
(b) Kings Park and Botanic Garden, West Perth WA 6005
ph: 480-3600 fax: 322-5064
interests: plant conservation biology, evolution, systematics, botanic gardens
- Hopwood, J M** ORD August 1989
(b) Mathematics Department, University of Western Australia, Nedlands WA 6907 ph: 380-3356
fax: 380-1028
E-mail: HOPWOOD@MATHS.UWA.EDU.AU
(h) 20 Shakespeare Street, Leederville WA 6007
ph: 444-4804
interests: climate [modelling, dynamics of tropical cyclones, palaeoclimatology], soils, wind erosion, palaeoclimatology, monsoons, surface temperature history, inversion of borehole temperature
- Horwitz, P H J** ORD July 1987
(b) Department of Environmental Management, Edith Cowan University, Joondalup Drive, Joondalup WA 6027
E-mail: P.Horwitz@cowan.edu.au
interests: inland aquatic ecology, invertebrate biogeography, invertebrate conservation
- Hos, D P C** ORD April 1974
(b) Unit 7, 21 McCabe Street, North Fremantle WA 6159
ph: 430-8460 fax: 430-8465
(h) 3 May Close, Mosman Park WA 6012 ph: 385-3505
interests: palynology [Australia, South East Asia], diatoms
- Hosken, D** STU March 1994 Nedlands WA

- Howden, P R ORD October 1963 Attadale WA
- Ingram, B S ORD April 1966
(b) 19 Rennington Street, Dianella WA 6062 ph: 276-2775
fax: 276-2710
(h) as above
interests: stratigraphic palynology
- Isted, W T C ORD December 1976 Mount Pleasant WA
- Jablonski, N G ORD October 1991 Nedlands WA
- James, S A STU November 1993 Woodlands WA
- Jasinska, E J ORD December 1992
(b) Department of Zoology, University of Western Australia, Nedlands WA 6907 ph: 380-3970
fax: 380-1029 E-mail: edytajj@uniwa.uwa.edu.au
(h) 42 Majella Road, Mirrabooka WA 6061 ph: 344-3931
interests: animals [groundwater, cave, wetlands], tree root-fauna associations, aquatic microinvertebrates, freshwater springs, developmental plasticity
- Jenkins, C F H HON July 1929 [1973] [Medallist 1966] Claremont WA
- Jenkins, E A HON July 1933 [1965] Claremont WA
- Johnson, G I ORD May 1990
(b) Metex Resources NC, P O Box 204, South Perth WA 6151 ph: 474-2939 fax: 474-2937
interests: earth sciences
- Johnston, D B ORD March 1987 Attadale WA
- Johnstone, M H ORD September 1949 Carlingford NSW
- Jones, E ASO
(h) 6 Gairloch Street, Applecross WA 6153 ph: 364-9702
interests: plants, native flora of WA
- Jones, M G K ORD April 1992
(b) WA State Agricultural Biotechnology Centre, School of Biological & Environmental Sciences, Murdoch University, Perth WA 6150 ph: 360-2424 fax: 310-3505
E-mail: mgkjones@Murdoch.edu.au
(h) ph: 316-1369
interests: plants [genetic engineering, biotechnology, molecular biology, tissue culture, transformation]
- Jones, R A C ORD April 1992 South Perth WA
- Keeley, G J ORD July 1984 Palmyra WA
- Keighery, G J ORD April 1976 Wanneroo WA
- Kendrick, G W ORD December 1965 Perth WA
- Kenneally, K F ORD March 1969 Como WA
- Kinnear, A C ORD November 1978 Wembley Downs WA
- Kinnear, J E ORD November 1978 Wembley Downs WA
- Klemm, V V ORD June 1987 Halls Head WA
- Koch, L E HON March 1958 [1989] Salters Point WA
- Ladd, P ORD April 1987
(b) School of Biological & Environmental Sciences, Murdoch University, Murdoch WA 6150 ph: 360-2219
fax: 310-4997 E-mail: ladd@esun1.Murdoch.edu.au
interests: plants, ecology, palaeoecology
- Lamont, B B ORD March 1972
(b) School of Environmental Biology, Curtin University of Technology, PO Box U1987, Perth WA 6102 ph: 351-7368
fax: 351-2495
interests: ecology, conservation and ecophysiology of native plants
- Lawrence, M E ORD June 1987 Forrestfield WA
- Leary, D E STU March 1994 Flagstaff Hill SA
- Lemson, K L STU Nedlands WA
- Lenanton, R J ORD August 1974 North Beach WA
- LeProvost, M I ORD June 1987 South Perth WA
- Lintern, M J ORD May 1987 Mount Hawthorn WA
- Littlejohn, M J ORD March 1956 Parkville VIC
- Loneragan, J F ORD November 1961 Murdoch WA
- Loneragan, N R ORD February 1981 Cleveland QLD
- Loneragan, W A ORD September 1963
(b) Department of Botany, University of Western Australia, Stirling Highway, Nedlands WA 6907
ph: 380-2216 fax: 380-1001
(h) 1 Desford Close, Shelley WA 6148 ph: 457-3238
interests: plants ecology, conservation, taxonomy, dendrochronology
- Longnecker, N ORD September 1993 Nedlands WA
- Lord, J H ORD November 1942
(h) 25 Hillway Street, Nedlands WA 6009 ph: 386-5795
interests: geology, mineral exploration
- Lund, M A ORD November 1993 Joondalup WA
- Luscombe, A F ORD May 1990 Carine WA
- Lynch, D A STU September 1990 Nedlands WA
- Lyons, T J ORD July 1988
(b) Biological & Environmental Sciences, Murdoch University, Murdoch WA 6150 ph: 360-2925
fax: 310-3505 E-mail: lyons@atmos.Murdoch.edu.au
interests: mesoscale meteorology, boundary layer studies, air pollution meteorology
- Macey, D J ORD September 1990
(b) Biological & Environmental Sciences, Murdoch University, Murdoch WA 6150 ph: 360-2363
fax: 310-3505 E-mail: macey@possum.Murdoch.edu.au
interests: animals physiology, chitons, iron metabolism, thalassemia, lampreys
- Macfarlane, T D ORD December 1973 Manjimup WA
- Main, A R HON July 1951 [1982] Nedlands WA
- Main, B Y ORD September 1952
(b) Zoology Department, University of Western Australia, Nedlands WA 6907 ph: 380-2239 fax: 380-1029
interests: arachnology, spiders, taxonomy, biogeography, life history strategies, environmental and social history of WA wheatbelt
- Majer, J D ORD November 1974
(b) School of Environmental Biology, Curtin University of Technology, P O Box U1987, Perth WA 6001
ph: 351-7964 fax: 351-2495
E-mail: jmajerj@info.curtin.edu.au
(h) 18 Catherine Street, Subiaco WA 6008 ph: 381-9281
interests: entomology, ants, conservation, environment, minesite restoration
- Manning, C R ORD December 1991 Applecross WA
- Marchant, N G ORD September 1963 Como WA
- Marsh, L M ORD November 1955
(b) WA Museum, Francis Street, Perth WA 6000
ph: 427-2751 fax: 328-8686
(h) 6 Lillian Street, Cottesloe WA 6011 ph: 383-2742
interests: taxonomy, echinoderms of Australia and Indo-Pacific, scleractinian corals, zoogeography
- Marshall, J K ORD June 1974 Wembley WA
- Masters, B K ORD June 1970
(b) PO Box 315, Capel WA 6271 ph: (097) 27-2474
fax: (097) 27-2670
(h) as above
interests: geology, mineral sands, environmental management [natural areas, dairy waste, catchments wetlands], environmental impact assessment, post-mining rehabilitation
- McArthur, W M ORD June 1951 Alfred Cove WA
- McCaw, W L ORD June 1986
(b) Science and Information Division, Department of Conservation & Land Management, Brain Street, Manjimup WA 6258 ph: (097) 71-1988 fax: (097) 77-1183
interests: fire behaviour, fire ecology, forest management, semi-arid woodlands
- McComb, A J ORD May 1963
(b) School of Biological & Environmental Science, Murdoch University, Murdoch WA 6150 ph: 360-2191
fax: 310-4997
interests: water quality inestuaries and near-shore marine systems
- McDonald, D STU Innaloo WA
- McGrath, J F ORD June 1984 Busselton WA
- McMillan, R P ORD May 1956
(h) 64 St Ives, Northshore Dampier Avenue, Kallaroo WA 6025 ph: 307-8973
interests: insects [buprestidae, formicidae, antiquilines], photography, environmental entomology
- McNamara, K J ORD September 1979
(b) WA Museum, Francis Street, Perth WA 6000
ph: 328-4411 fax: 328-8686
E-mail: mcnamk@muswa.dialix.oz.au
interests: palaeontology, evolutionary theory
- Mees, G F ORD May 1959 Busselton WA
- Merrifield, H E ORD November 1969 Rockingham WA

- Merrilees, D** HON July 1959 [1979]
(h) RMB 256, Manjimup WA 6258 ph: (097) 72-3587
interests: geology, quaternary studies, archaeozoology
- Millington, A J** ORD August 1952 Kununurra WA
- Mills, C H** ORD October 1986 Bassendean WA
- Milne, V A** ORD April 1987 Albany WA
- Moore, L S** ORD March 1990
(b) Groundwater and Environment Branch, Water Authority, P O Box 100, Leederville WA 6902
ph: 420-2308 fax: 420-3176
(h) 4 Burrendah Boulevard, Willetton WA 6155
interests: stromatolites, environmental management, lake ecology, cyanobacteria
- Moore, R D** ORD March 1994 Nedlands WA
- Morgan, B** STU
(h) 140 Townshend Road, Subiaco WA 6008 ph: 382-3548
interests: plant pathology
- Morgan, K H** ORD August 1961
(b) K H Morgan and Associates, Bentley Business Centre, Unit 10, 4 Queen Street, Bentley WA 6102 ph: 384-3689/356-5455 fax: 351-9853
(h) 3 Jennifer Way, Rossmoyne WA 6148 ph: 354-3689
interests: groundwater hydrogeology, geological exploration and valuation, industrial water supply [particularly mining], environmental hydrogeology
- Morgan, W R** ORD Como WA
- Morrison, D A** ORD April 1987 Scarborough WA
- Morrison, P F** ORD October 1993 South Perth WA
- Moulds, M S** LIF July 1965
(b) Entomology Department, Australian Museum, P O Box A285, Sydney South NSW 2000 ph: (02) 339-8221 fax: (02) 360-4350 E-mail: maxm@amsq.austmus.oz.au
(h) 16 Park Avenue, Waitara NSW 2077 ph: (02) 487-2792
interests: entomology [cicadas, moths, butterflies]
- Muir, B G** ORD August 1967
(b) Muir Environmental, 1400 Coulston Road, Boya WA 6056 ph: 299-6804 fax: 299-8302
(h) as above
interests: environmental impact assessment and rehabilitation [especially of mines and quarries], environmental policy, statutory compliance auditing, environmental toxicology, artificial wetlands, ecology of tropical environments
- Murphy, D P** ORD May 1993
(b) Environmental Officer, Western Mining Corporation, LMK Operations, P O Box 22, Leinster WA 6437 ph: (090) 37-9929 fax: (090) 37-9090
(h) P O Box 194, Leinster WA 6437 ph: (090) 37-9929
interests: environmental management, avian biology, ecophysiology of arid-zone fauna, arid-zone ecology
- Myers, J S** ORD September 1987 East Perth WA
- Nash, D W** ORD August 1972
(b) D W Nash & Associates, 86 Marlow Street, Wembley WA 6014 ph: 387-4202 fax: 387-1212
(h) 86 Marlow Street, Wembley WA 6014 ph: 387-4202 fax: 387-1212
interests: information technology, scientific computing [earth sciences], general computing
- Noel, D** ORD August 1989
(b) PO Box 27, Subiaco WA 6008 ph: 385-3400 fax: 385-1612
interests: nut and tree crops, earth expansion, human society, ore genesis
- O'Shea, J E** ORD November 1992
(b) Zoology Department, University of Western Australia, Nedlands WA 6907 ph: 380-2242 fax: 380-1029
E-mail: joshea@uniwa.uwa.edu.au
interests: vertebrate morphology, reptiles, bats
- Oldham, J A** ORD June 1987
(b) 44 Berkeley Crescent, Floreat Park WA 6014 ph: 387-8355 fax: 387-8355
interests: environmental management, natural resources management
- Oliver, K R** ORD April 1994 Wilson WA
- Orsini, J P** ORD June 1992
(b) National Threatened Species Network, 78 Stirling Highway, Perth WA 6000 ph: 384-3756 fax: 220-0652
(h) 15 Hooley Street, Swanbourne WA 6010 ph: 384-3756 fax: 220-0652
interests: wildlife conservation, endangered species, biodiversity, malleefowl, whales, flora, environmental policy and legislation, environmental education
- Osborne, J M** ORD September 1985 Perth WA
- Osman, A H** ORD August 1962
(h) 24 Stanhope Road, Killara NSW 2071
ph: (02) 498-3615 fax: (02) 418-2132
interests: geology, South East Asia, reading
- Oxnard, C** ORD October 1993 Nedlands WA
- Palmer, L** ORD
(b) University Department of Paediatrics, GPO Box D184, Perth WA 6001 ph: 340-8176 fax: 388-2097
E-mail: lyle@ichr.uwa.edu.au
(h) Unit 2, 165 Roberts Road, Subiaco WA 6008
ph: 382-3205
interests: genetic epidemiology of asthma, genetic epidemiology of cerebral palsy, paediatric epidemiology
- Parker, C A** ORD August 1959 [Medallist 1986] Nedlands WA
- Parker, I N** ORD August 1988 South Fremantle WA
- Pate, J S** ORD October 1977 Nedlands WA
- Pearce, A F** ORD December 1981
(b) Division of Oceanography, P O Box 20, North Beach WA 6020 ph: 246-8288 fax: 246-8233
E-mail: alan.pearce@per.ml.csiro.au
(h) 8 Currajong Road, Duncraig WA 6023 ph: 246-2910
interests: oceanography (general), ocean currents, Leeuwin current, satellite remote sensing of the oceans
- Pearce, R H** ORD March 1955 Kalamunda WA
- Pearman, G I** ORD September 1963
(b) Chief, Division of Atmospheric Research, CSIRO, PMB #1, Mordialloc VIC 3195 ph: (03) 586-7650
fax: (03) 586-7553 E-mail: chief@dar.csiro.au
(h) 67 Larnook Crescent, Ascendale VIC 3195
ph: (03) 580-5960
interests: global composition of the atmosphere, global carbon cycle, climate variability and change
- Peet, L J** ORD August 1965 Dalkeith WA
- Perry, G** ORD June 1966 Como WA
- Perry, M W** ORD November 1971 South Perth WA
- Playford, P E** ORD August 1952
(b) Geological Survey of WA, 100 Plain Street, East Perth WA 6004 ph: 222-3157 fax: 222-3633
E-mail: p.playford@dme.wa.gov.au
(h) 102 Thomas Street, Nedlands WA 6009 ph: 386-4169
interests: geology, history, anthropology, heritage
- Podger, F** ORD October 1993 Como WA
- Poole, W E** ORD April 1951 Dickson ACT
- Potter, I C** ORD July 1981 Salters Point WA
- Prendergast, W F** LIF April 1985 Claremont WA
- Price, L K** ORD March 1987 Belmont WA
- Price, M** STU
(b) Alan Tingay and Associates, 35 Labouchere Road, South Perth WA 6151 ph: 474-1300 fax: 474-3394
(h) 47 Regent Avenue, Mt Pleasant WA 6153
ph: 364-3149
interests: zoology, environmental science
- Prider, R T** HON July 1932 [1976] [Medallist 1970] Nedlands WA
- Purcell, P G** ORD April 1989
(b) 141 Hastings Street, Scarborough WA 6019
ph: 245-2155 fax: 341-8679
(h) as above
interests: petroleum exploration, conservation and development issues, aboriginal land rights issues
- Quilty, P G** ORD June 1962
(b) Australian Antarctic Division, Channel Highway, Kingston TAS 7150 ph: (002) 32-3205 fax: (002) 32-3351
E-mail: pat_qui@antdiv.gov.au
(h) 211 Nelson Road, Mt Nelson TAS 7007
ph: (002) 25-3217
interests: palaeontology, antarctica, early maritime exploration of Australia, music
- Ravine, D** ORD June 1983 Cyncoed, Cardiff, Wales

- Rice, G E ORD September 1980 Ringwood East VIC
- Rich, P J ORD April 1991
(b) University of the Americas, Cholula, Puebla 72820 MEXICO
(h) Hoover Institution, Stanford University, Stanford California USA
interests: computers in education
- Ride, W D L ORD September 1958 Hughes ACT
- Ridsdill-Smith, T J ORD December 1980 Wembley WA
- Roberts, A STU September 1994 Nedlands WA
- Roberts, J D ORD September 1993
(b) Department of Zoology, University of Western Australia, Nedlands WA 9607 ph: 380-2224 fax: 380-1029 E-mail: droberts@uniwa.uwa.edu.au
(h) 106 Holland Street, Wembley WA 6014 ph: 387-2471
interests: amphibians, conservation, biogeography, evolution [particularly frogs]
- Roe, R ORD July 1969 Kensington WA
- Rohl, L ORD Wembley WA
- Rook, M K ORD April 1986 North Perth WA
- Rooke, I J ORD July 1982 Margaret River WA
- Sanders, C C ORD June 1968 Perth WA
- Sappal, K K ORD March 1991 Perth WA
- Saunders, D A ORD April 1983 Guildford WA
- Scott, J ORD February 1991 Maida Vale WA
- Scott, J K ORD September 1978
(b) CSIRO Division of Entomology, Private Bag, PO Wembley WA 6014 ph: 387-0644 fax: 387-0646 E-mail: JOHNS@CCMAR.CSIRO.AU
interests: biological control of weeds
- Scott, W D ORD September 1991 Murdoch WA
- Searle, D J ORD June 1987 Dalkeith WA
- Seddon, G ORD June 1962
(b) Centre Studies Aust. Literature, Department of English, University of Western Australia, Nedlands WA 6907 ph: 380-2255 fax: 380-1030
(h) 'Lemarville', 186 High Street, Fremantle WA 6160 ph: 335-9005 fax: 335-9005
interests: environmental planning and design, cultural history, history of science
- Semeniuk, C A ORD October 1986 Warwick WA
- Semeniuk, V ORD March 1979 Warwick WA
- Shaw, S E ORD July 1959 North Ryde NSW
- Shearer, B L ORD May 1968 Como WA
- Shivas, R G ORD July 1988 Doubleview WA
- Shugg, H B ORD November 1959
(h) 5 McCallum Crescent, Ardross WA 6153 ph: 364-1226
interests: population control, maintenance of biodiversity, public administration
- Smith, E B J ORD October 1969 Attadale WA
- Smith, G G HON July 1951 [1979] Claremont WA
- Smith, L A ORD May 1972 Perth WA
- Sproul, A N ORD July 1978
(h) 38 Coogee Road, Ardross WA 6153 ph: 364-4349
interests: general entomology [particularly control of insects of agricultural importance]
- Stace, H ORD May 1993
(b) Botany Department, University of Western Australia, Nedlands WA 6907 ph: 380-1862 fax: 380-1001 E-mail: hmstace@uniwa.uwa.edu.au
(h) 18/370 Barker Road, Subiaco WA 6008 ph: 382-4385
interests: plant genetics and evolution
- Start, A N ORD May 1979 Roleystone WA
- Steer, B T ORD July 1987 Como WA
- Stephens, L J ORD August 1985 Roleystone WA
- Stephenson, N C ORD June 1969
(b) Department of Geology & Geophysics, University of New England, Armidale NSW 2351 ph: (067) 72-2860 fax: (067) 71-2898
interests: metamorphic petrology
- Stoneman, G ORD October 1988
(b) Department of Conservation & Land Management, Hackett Drive, Crawley WA 6009 ph: 442-0321 fax: 389-8603
(h) 1 Lowanna Way, City Beach WA 6015 ph: 385-7108
interests: forest science, forest ecology, forest hydrology, silviculture
- Sweetingham, M W ORD April 1990 East Fremantle WA
- Tassell, C B ORD July 1976 Launceston TAS
- Taylor, J C ORD May 1970
(h) 8 Circe Circle, Dalkeith WA 6009 ph: 386-1633
- Teichert, C HON July 1938 [1975]
(h) 5505 North 10th Street, Arlington Virginia 22205 USA
interests: geology, palaeontology
- Terrill, S E HON July 1928 [1973] WA
interests: family history
- Thomas, L N ORD April 1987 East Fremantle WA
- Tingay, A ORD May 1991 Darlington WA
- Tommerup, I C ORD April 1994
(b) CCMAR, CSIRO, Private Bag, Post Office, Wembley WA 6014
interests: plant/fungal molecular biology, ecosystem sustainability
- Trendall, A F ORD May 1963 Applecross WA
- Triffitt, M A ORD November 1987 Nedlands WA
- Underwood, R INS Como WA
- Unkovich, M J ORD October 1994 Nedlands WA
- Utting, E P LIF May 1963 Mosman Park WA
- Walker, C J STU March 1994 South Perth WA
- Walker, D I ORD August 1989
(b) Botany Department, University of Western Australia, Nedlands WA 6907 ph: 380-2089 fax: 380-1001 E-mail: diwalker@uniwa.uwa.edu.au
interests: marine botany, education
- Wallace, G I ORD April 1980 Geraldton WA
- Wardell-Johnson, G W ORD November 1987 Bridgetown WA
- Warren, S
(h) 24 Richardson Avenue, Dynnyrne TAS 7005
interests: geotectonics
- Watts, J STU Kelmscott WA
- Whitaker, D ORD November 1993 Kingsley WA
- Wilkinson, D S ORD April 1992 Mt Hawthorn WA
- Willmott, S P ORD June 1962 Forrestfield WA
- Wills, R T ORD April 1990
(b) W. A. Herbarium, P O Box 104, Como WA 6152 ph: 334-0500 fax: 334-0515 E-mail: rwills@wa.erin.gov.au
(h) 56 Inverness Crescent, Menora WA 6050 ph: 271-8901
interests: ecology, conservation, plant disease, fire ecology, mycology, climate change, computing, geographic information systems
- Withers, P C ORD April 1987
(b) Zoology Department, University of Western Australia, Nedlands WA 6907 ph: 380-2235 fax: 380-1029 E-mail: pwithers@uniwa.uwa.edu.au
(h) 2 Lookout Road, Kalamunda WA 6076 ph: 293-3115
interests: arid zone physiology and ecology of animals, natural history [frogs, lizards, birds, mammals], computing, ecophysiology
- Woodall, R ORD September 1955
(b) Western Mining Corporation, P O Box 409, Unley SA 5061 ph: (08) 372-7220 fax: (08) 372-7250
(h) Wonnaminta House, P O Box 9A, Crafrers SA 5152 ph: (08) 339-4550 fax: (08) 370-9461
interests: geology, geoscience, exploration management, mineral resources, petroleum resources
- Woods, P J ORD June 1987 Cottesloe WA
- Wooler, S ORD May 1990 Rossmoyne WA
- Wooler, R D ORD October 1993 Murdoch WA
- Wurm, P A S ORD June 1987 Casuarina NT
- Wycherley, P R ORD March 1972
(h) 160 Nicholson Road, Subiaco WA 6008 ph: 381-8407
interests: economic and amenity botany, arboriculture, conservation, parks and recreation
- Youngson, W K ORD June 1987 Keysbrook WA
- Yu, B ORD April 1993 Sunnybank QLD

Index of Interests

- aboriginal studies Crawford, I M
 agricultural science Jones, F G W
 agriculture: entomological Sproul, A N
 agroforestry Congdon, R A; Farrington, P
 agronomy Gladstones, J S
 air pollution Lyons, T J
 algae: Borowitzka, M A
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 animals: ants Majer, J D
 animals: archaeozoology Merrilees, D
 animals: bats O'Shea, J E
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 animals: corals (scleractinian) Marsh, L M
 animals: echinoderms (Australia and Indo-Pacific) Marsh, L M
 animals: frogs Roberts, J D; Withers, P C
 animals: groundwater Jasinska, E J
 animals: groundwater, cave, wetlands Jasinska, E J
 animals: insects Moulds, M S
 animals: invertebrates Horwitz, P H J; Bayly, I A E
 animals: lampreys Macey, D J
 animals: lizards Withers, P C
 animals: malleefowl Orsini, J P
 animals: pests Jones, F G W
 animals: physiology Macey, D J; Withers, P C
 animals: whales Orsini, J P
 Antarctica Quilty, P G
 anthropology Playford, P E
 aquatic microinvertebrates Jasinska, E J
 arachnology Harvey, M S; Main, B Y
 arboriculture Wycherley, P R
 archaeology Crawford, I M; Hallam S
 archaeozoology Merrilees, D
 arid-zone: ecology Burrows, N D; Finucane, S J
 arid-zone: ecophysiology Bradshaw, S D; Murphy, D;
 Withers, P C
 astronomy Birch, P V
 astrophysics De Laeter, J R
 atmosphere: boundary layers, air pollution Lyons, T J
 atmosphere: global composition, carbon cycle Pearman, G I
 bats O'Shea, J E
 bioactive molecules Borowitzka, M A
 biochemistry Guppy, M
 biodiversity Orsini, J P; Shugg, H B
 biogeography Gentili, J; Roberts, J D
 biogeography: birds Burbidge, A H
 biogeography: invertebrates Horwitz, P H J
 biogeography: spiders Main, B Y
 biological control: weeds Scott, J K
 biology: arid zone Finucane, S J
 birds: biology Burbidge, A H; Murphy, D
 birds: conservation Burbidge, A H
 botany: Davison, E
 botanic gardens: Hopper, S
 chemistry: development in South East Asia Cannon, J R
 chemistry: education, environmental Garnett, P J
 chemistry: natural products Cannon, J R
 climatology Gentili, J; Wills, R T
 climatology: modelling, dynamics of tropical cyclones,
 palaeoclimatology Hopwood, J M
 climatology: variability, change Pearman, G I
 coastal geoscience Burne, R V
 computing Nash, D W; Rich, P; Wills, R T; Withers, P C
 conservation Abensperg-Traun, M; Dixon, K W; Hatcher, B G;
 Loneragan, W; Purcell, P; Roberts, J D; Wills, R T;
 Wycherley, P R
 conservation: insects Majer, J D
 conservation: invertebrates Horwitz, P H J
 conservation: plants Hopper, S; Lamont, B B
 conservation: threatened birds Burbidge, A H
 conservation: wildlife Orsini, J P
 corals Borowitzka, M A; Marsh, L M
 cultural history Seddon, G
 cyanobacteria Moore, L S
 cyclones Hopwood, J M
 dendrochronology Loneragan, W
 development issues Purcell, P
 developmental plasticity Jasinska, E J
 diatoms Hos, D P C
 disease: plants Bathgate, J A; Wills, R T
 drylands: solute leaching, movements Bourgault du
 Coudray, P L
 earth expansion Noel, D
 earth science Johnson, G
 earth science: computing Nash, D W
 ecology Abbott, I J; Hallam, S; Hart, R P; Wills, R T
 ecology: aquatic Froend, R H
 ecology: arid zone Burrows, N D; Finucane, S J; Murphy, D;
 Withers, P C
 ecology: benthic Hatcher, B G
 ecology: coral reef Borowitzka, M A
 ecology: ecosystem sustainability Tommerup, I C
 ecology: estuaries Hodgkin, E P
 ecology: fire McCaw, W L; Wills, R T
 ecology: forests Stoneman, G
 ecology: inland Horwitz, P H J
 ecology: invertebrates Abensperg-Traun, M
 ecology: lakes Moore, L S
 ecology: management Froend, R H
 ecology: palaeoecology Ladd, P
 ecology: plants Bell, D T; Congdon, R A; Foulds, W; Froend, R
 H; Gordon, D; Ladd, P; Lamont, B B; Loneragan, W
 ecology: Rottneest Island Dodd, J
 ecology: terrestrial Bamford, M J; Froend, R H; Withers, P C
 ecology: tropical Muir, B G
 ecology: viticulture Gladstones, J S
 ecology: WA granites Bayly, I A E
 ecology: wetlands Balla, S A; Froend, R H
 ecophysiology Bradshaw, S D; Gordon, D; Lamont, B B;
 Murphy, D; Withers, P C
 education: chemistry, environment Garnett, P J
 education: environment Orsini, J P
 education: science De Laeter, J R; Rich, P; Walker, D I
 endangered species Burbidge, A H; Orsini, J P
 endocrinology: comparative Bradshaw, S D
 engineering: geology Gray, N M
 entomology: agricultural control Sproul, A N
 entomology: ants, conservation Majer, J D
 entomology: cicadas, moths, butterflies Moulds, M S
 entomology: environmental McMillan, R P
 environment: policy, legislation, education Orsini, J P
 environment: rehabilitation, mine sites Bamford, M J; Majer, J D
 environment: rural land degradation and management
 Conacher, A J
 environment: urban Goble-Garratt, D
 environmental chemistry Garnett, P J
 environmental entomology McMillan, R P
 environmental history: WA wheatbelt Main, B Y
 environmental hydrogeology Morgan, K H
 environmental impact assessment Finucane, S J; Hart, R P;
 Hilliard, R W; Masters, B K; Muir, B G
 environmental management Hart, R P; Hilliard, R W; Masters,
 B K; Moore, L S; Murphy, D; Oldham, J A
 environmental planning, design Seddon, G
 environmental policy Muir, B G
 environmental science Price, M
 epidemiology: asthma, cerebral palsy, paediatrics Palmer, L
 estuaries: ecology Hodgkin, E P
 estuaries: water quality McComb, A J
 evolution Hopper, S; McNamara, K J; Roberts, J D; Stace, H
 exploration Lord, J H; Morgan, K H; Purcell, P; Woodall, R
 family history Terrill, S E
 fire: ecology Bamford, M J; Burrows, N D; McCaw, W L;
 Wills, R T
 fire: management Burrows, N D

- fire: small mammals Bamford, M J
 fisheries Hatcher, B G
 flora: native Jones, E; Jones, F G W
 floriculture Considine, J A
 forestry Abbott, I J; Burrows, N D; Davison, E; Stoneman, G
 forestry: agroforestry Congdon, R A; Farrington, P
 forestry: ecology Stoneman, G
 forestry: hydrology Stoneman, G
 forestry: management Burrows, N D; McCaw, W L
 forestry: silviculture Stoneman, G
 freshwater springs Jasinska, E J
 fungi: molecular biology Tommerup, I C
 genetic engineering: plants Jones, M G K
 genetics: epidemiology of asthma, cerebral palsy Palmer L
 genetics: plants Cowling, W A; Stace, H
 geochemistry Davy, R
 geographic information systems Wills, R T
 geology Backhouse, J; Davy, R; Merrilees, D; Noel, D;
 Osman, A H; Playford, P E; Stephenson, N C; Teichert, C;
 Woodall, R
 geology: economic Davy, R
 geology: engineering Gray, N M
 geology: exploration Davy, R; Lord, J H; Morgan, K H;
 Woodall, R
 geology: marine Hatcher, B G
 geology: mineral sands Masters, B K
 geology: Palaeozoic and Mesozoic sedimentary rocks in WA
 Backhouse, J
 geology: quaternary Brown, R G; Merrilees, D
 geology: regional Gray, N M
 geology: resources Woodall, R
 geology: sedimentology Brown, R G
 geology: South East Asia Osman, A H
 geology: valuation Morgan, K H
 geophysics Gray, N M
 geoscience: coastal Burne, R V
 geotectonics Warren, S
 habitat restoration Dixon, K W
 heritage Playford, P E
 history Bridge, P J; Playford, P E
 history: environmental and social, WA wheatbelt Main, B Y
 history: family Terrill, S E
 history: science Seddon, G
 human society Noel, D
 hydrology: catchments Farrington, P
 hydrology: forests Stoneman, G
 hydrology: groundwater Morgan, K H
 hydrology: hydrogeology Morgan, K H
 information technology Nash, D W
 insects: buprestidae, formicidae, antequilines, photography
 McMillan, R P
 iron metabolism Macey, D J
 islands Abbott, I J
 lakes: ecology Moore, L S
 land management Conacher, A J
 limnology Bayly, I A E
 management: natural resources, environment Oldham, J A
 management: waterways Atkins, R P
 management: wetlands Froend, R H
 mangroves: Gordon, D
 marine biology: seagrass epiphytes Borowitzka, M A
 marine botany Walker, D I
 marine geology Hatcher, B G
 marine systems: water quality, near-shore McComb, A J
 marine: early maritime exploration Quilty, P G
 metabolism: biochemistry Guppy, M; Withers, P C
 meteorology: air pollution, mesoscale Lyons, T J
 microbialites Burne, R V
 migrations Gentili, J
 mineral exploration Lord, J H
 mineral resources Woodall, R
 mineral sands Masters, B K
 mineralogy Bridge, P J
 mining: industrial water supply Morgan, K H
 molecular biology: fungi Tommerup, I C
 molecular biology: plants Jones, M G K; Tommerup, I C
 monsoons Hopwood, J M
 music Quilty, P G
 mycology Davison, E; Wills, R T
 myrmecophagy Abensperg-Traun, M; Withers, P C
 natural history: editing texts George, A S
 natural history: terrestrial vertebrates Withers, P C
 natural products Cannon, J R
 natural resource management Briggs, I M; Oldham, J A
 natural science Goble-Garratt, D
 nematodes parasitic on plants Jones, F G W
 oceanography Hatcher, B G; Pearce, A F
 ore genesis Noel, D
 paediatrics: epidemiology Palmer, L
 palaeoclimatology: monsoons, surface temperature history,
 inversion of borehole temperature: climatology
 Hopwood, J M
 palaeoecology Ladd, P
 palaeontology McNamara, K J; Quilty, P G; Teichert, C
 palaeontology: Palaeozoic and Mesozoic sedimentary rocks
 Backhouse, J
 palynology: Australia, South East Asia, diatoms Hos, D P C
 palynology: Palaeozoic and Mesozoic sedimentary rocks
 Backhouse, J
 palynology: stratigraphic Ingram, B S
 parks and recreation Wycherley, P R
 pathology: plants Bathgate, J A; Davison, E.; Morgan, B
 petroleum exploration Purcell, P
 petroleum resources Woodall, R
 petrology: metamorphic Stephenson, N C
 philosophy of science Bradshaw, S D
 photosynthesis: Gordon, D
 physics: mass spectrometry De Laeter, J R
 physiology: animals Bradshaw, S D; Macey, D J; Withers, P C
 physiology: plants Gordon, D
 plants: aquatic Froend, R H
 plants: banksia woodland Dodd, J
 plants: biological control Scott, J K
 plants: biotechnology Jones, M G K
 plants: breeding Considine, J A; Dixon, K W; Gladstones, J S
 plants: conservation Dixon, K W; Hopper, S
 plants: conservation, ecophysiology Lamont, B B
 plants: development, productivity, improvement
 Considine, J A
 plants: disease Bathgate, J A; Hart, R P; Wills, R T
 plants: ecology Bell, D T; Congdon, R A; Foulds, W;
 Froend, R H; Ladd, P; Lamont, B B; Loneragan, W
 plants: economic and amenity botany Wycherley, P R
 plants: ecophysiology Lamont, B B
 plants: flora Jones, E; Jones, F G W; Orsini, J P
 plants: genetic engineering Jones, M G K
 plants: genetics, evolution Cowling, W A; Jones, M G K;
 Stace, H
 plants: germplasm storage Dixon, K W
 plants: marine botany Walker, D I
 plants: micropropagation Dixon, K W
 plants: molecular biology Jones, M G K; Tommerup, I C
 plants: native flora of WA Jones, E; Jones, F G W
 plants: nut and tree crops Noel, D
 plants: nutrient cycling Congdon, R A
 plants: parasitic nematodes Jones, F G W
 plants: pathology Bathgate, J A; Davison, E; Morgan, B
 plants: productivity Congdon, R A
 plants: rainforest Congdon, R A
 plants: seed germination Dixon, K W
 plants: systematics of Australian flora George, A S
 plants: terrestrial Dodd, J; Froend, R H
 plants: tissue culture Jones, M G K
 plants: transformation Jones, M G K
 plants: water relations Froend, R H
 plants: water use Farrington, P
 plants: weed biological control Dodd, J
 plants: weeds Scott, J K
 plants: wetlands Congdon, R A
 population control Shugg, H B
 prehistoric settlement: Hallam, S
 public administration Shugg, H B

- rainforest Congdon, R A
 regional geology Gray N M
 regional resource planning Briggs I M
 rehabilitation: mine sites Bamford, M J; Masters, B K
 resources: mineral, petroleum Woodall, R
 resources: utilisation Goble-Garratt, D
 Rottnest Island: ecology Dodd, J
 salinity Bourgault du Coudray, P L; Farrington, P
 satellite remote sensing Pearce, A F
 science: education De Laeter, J R
 science: history Seddon, G
 science: policy Abbott, I J
 sedimentology Brown, R G
 seeds: germination Considine, J A; Dixon, K W
 seeds: physiology, dormancy Considine, J A
 silviculture Stoneman, G
 social history: WA Wheatbelt Main, B Y
 soils: biology Abbott, I J
 soils: solute leaching, macropores, salinity control, drylands
 Bourgault du Coudray, P L
 soils: wind erosion Hopwood, J M
 soils: soil/slope relationships Conacher, A J
 sponges Borowitzka, M A
 stratigraphy: Palaeozoic and Mesozoic sedimentary rocks
 Backhouse, J
 stromatolites Burne, R V; Moore, L S
 taxonomy Dixon, K W; Loneragan, W
 taxonomy: arachnids Harvey, M S
 taxonomy: echinoderms Marsh, L M
 taxonomy: plants George, A S; Hopper, S
 taxonomy: spiders Main, B Y
 thalassemia Macey, D J
 toxicology Borowitzka, M A
 tree root-fauna associations Jasinska, E J
 tropical fruit: growth, development Considine, J A
 urban environments Goble-Garratt, D
 viticulture Gladstones, J S
 water quality: estuaries, near-shore marine systems
 McComb, A J
 water resources Briggs, I M
 water: hydrology Morgan, K H
 water: industrial water supply, mining Morgan, K H
 waterways: management Atkins, R P
 weeds: biological control Dodd, J
 wetlands Congdon, R A; Finucane, S J; Masters, B K
 wetlands: artificial Muir, B G
 wetlands: ecology Balla, S A; Froend, R H
 wetlands: fauna Jasinska, E J
 wetlands: management Froend, R H
 wildlife Hart, R P
 woodlands: semi-arid McCaw, W L
 zoogeography: scleractinian corals Marsh, L M
 zoology Bayly, I A E; Price, M; Withers, P C

Recent Advances in Science in Western Australia

Earth Sciences

This study by J Clarke, of Western Mining Corporation, confirms the great age of the landscape of the Yilgarn Craton. The relict saprolite dates back to the Late Permian-Middle Jurassic. Stripping of this regolith occurred in the Middle Jurassic-Early Eocene during the formation of the palaeodrainage system. About 400 m of material was denuded from the craton to infill adjoining sedimentary basins, and further deep weathering occurred concurrently with erosion. Increasing aridity led to disorganization of the drainage to form a chain of lakes. Aridity increased in the Kambalda area in the Pliocene, leading to the establishment of the present-day semi-arid geomorphic regime. However, aridity has persisted for only 2% of the history of the Kambalda landscape, and arid geomorphic models are only appropriate for understanding the most recent evolution of the regolith.

Clarke J D A 1994 Geomorphology of the Kambalda region, Western Australia. *Australian Journal of Earth Sciences* 41:229-239.

This thematic issue, edited by N Exon (AGSO, Canberra) documents various studies of the Mesozoic rocks of the North West Shelf, based on samples and seismic profiles acquired on two cruises of the AGSO research vessel *Rig Seismic*. Six papers examine palaeontology, one examines sedimentary petrology, one examines igneous petrology, three examine seismic profiling, and one examines the Wallaby profile. There is also an overview of the shelf and a synthesis of the results of the various papers. This volume provides an important contribution to our understanding of a major petroleum province.

Exon N F (Editor) 1994 Thematic issue: Geology of the outer North West Shelf, Australia. *AGSO Journal of Australian Geology & Geophysics* 15:1-190.

D Lowe, of Stanford University (USA), considers that three well-documented occurrences of stromatolites older than 3.2 Ga are abiotic. Small conical structures in the Strelley Pool chert (Warrawoona Group, WA, 3.5 - 3.2 Ga) probably formed through evaporitic precipitation. A domal structure from the North Pole chert (also Warrawoona Group) formed by soft-sediment deformation. Domal and pseudocolumnar structures in laminated chert (Onverwacht Group, South Africa, 3.5 - 3.3 Ga) probably formed through inorganic precipitation.

Lowe D R 1994 Abiological origin of described stromatolites older than 3.2 Ga. *Geology* 22:387-390.

Most Neoproterozoic and Phanerozoic basins in Western Australia can be classified as Neoproterozoic, Palaeozoic or Mesozoic-Cainozoic based on their age of dominant fill and tectonic activity. This paper by R Hocking (GSWA, Perth) rationalizes the basin subdivisions using a common set of descriptive terms. The Savory, Amadeus, Officer and possibly the Yeneena and Karara Basins are Neoproterozoic. The Gunbarrel, Southern Bonaparte, Ord, Canning and Southern Carnarvon Basins are Palaeozoic. The Northern Bonaparte, Browse, Roebuck and Northern Carnarvon

Basins (together comprising the Westralian Superbasin) are Mesozoic-Cainozoic. The Perth Basin (with its outlier, the Collie Basin) contains both Palaeozoic and Mesozoic elements, while the Eucla and Bremer Basins are primarily Cainozoic depocentres.

Hocking R M 1994 Subdivisions of Western Australian Neoproterozoic and Phanerozoic sedimentary basins. *Geological Survey of Western Australia Record* 1994/4.

G Le Blanc Smith (GSWA, Perth) describes the coal resources of the Collie Basin, a fault-bounded, post-depositional pull-apart basin preserved as a consequence of right-lateral shear in a transitional setting. The 226 km² basin contains about 1200 m of Permian siliciclastics overlain by a veneer of Cretaceous rocks. The oldest Permian rocks were laid down in a glaciofluvial and glaciolacustrine setting, with fluvial to upper delta-plain alluvial coal deposition constituting the balance of the succession. The coal resources total 2400 Mt and are currently mined in four opencut and three underground mines; almost 80% is used for power generation. Over the past 100 years, about 100 Mt of coal has been produced.

Le Blanc Smith G 1993 Geology and Permian coal resources of the Collie Basin, Western Australia. *Geological Survey of Western Australia. Report* 38.

A remarkably well-preserved Frasnian radiolarian fauna is described by J C Aitchison (University of Sydney), from carbonate concretions in the Gogo Formation. It is the best preserved and most diverse Frasnian assemblage yet documented, with 57 species (41 new) assigned to 14 genera. All elements of the fauna are common, but it is dominated by ceratohiscids of which 11 are new species.

Aitchison J C 1993 Devonian (Frasnian) radiolarians from the Gogo Formation, Canning Basin, Western Australia. *Palaeontographica Abt. A* 228:105-128.

The incisoscutid arthrodire *Gogosteus sarahae* gen. et sp. nov. is described and illustrated by J Long (Western Australian Museum). This taxon, like many of the superbly preserved arthrodires from the Gogo Formation, is known from only a single specimen. It is represented by most of the headshield, trunkshield and dentition; the bones are uncrushed and preserved in three dimensions. As a result of the new material, the family Incisoscutidae Denison 1984 is redefined and the new superfamily Incisoscutioidea is defined to include Incisoscutidae and Camuropiscidae.

Long J A 1994 A second incisoscutid arthrodire (Pisces, Placodermi) from the Late Devonian Gogo Formation, Western Australia. *Alcheringa* 18:59-69.

Deep seismic reflection and magnetic data were collected along a 75 km traverse across the Darling Fault Zone by researchers from Curtin University and the University of Western Australia; 50 km of the traverse was over the Archaean Yilgarn Craton and 25 km was over the Perth Basin. The seismic data suggest that the crust beneath the western Yilgarn Craton is divided vertically into three structural zones. From 0 to 7-9 km, there is a zone of thin-skinned compressional tectonism expressed

as a series of thrusts, which links to a detachment surface at about 7-9 km depth. At 7-9 to 25 km, there is a zone with several minor detachments and a large intrusive igneous body. From 25 to 40 km, there is a zone of continuous seismic events that dip east at about 25°. The seismic data provide a good fault plane image of the Phanerozoic Darling Fault, which is distinct from the Precambrian proto-Darling Fault that is interpreted to coincide with a wide, non-reflecting zone extending west beneath the Perth Basin.

Middleton M F, Wilde S A, Evans B J, Long A, Dentith M & Morawa M 1995 Implications of a geoscientific traverse over the Darling Fault Zone, Western Australia. *Australian Journal of Earth Sciences* 42:83-93.

Correlation of rocks in the Savory Basin with those of adjacent basins is impeded by poor outcrop and lack of subsurface information, but two new correlations by collaborators from Macquarie University and GSWA (Perth) clarify the age and relationships of the Savory basin. First, the Skates Hill Formation contains distinctive stromatolites (*Acaciella australica*) previously recorded from the Bitter Springs Formation of the Amadeus basin. Second, the intergrading sandstone-diamictite of the Boondawari Formation is very similar to the intergrading Pioneer Sandstone-Olympic Formation of the Amadeus Basin; this correlation is also supported by carbon isotope chemostratigraphy.

Walter M R, Grey K, Williams I R & Calver C R 1994 Stratigraphy of the Neoproterozoic to Early Palaeozoic Savory Basin, Western Australia, and correlation with the Amadeus and Officer Basins. *Australian Journal of Earth Sciences* 41:533-546.

The Archaean supracrustal sequence at Forrestania contains at least five komatiitic belts, which can be traced along strike for over 30 km. Lithologies range from olivine cumulates, which crystallized at the interface between substrate and flowing lava, to spinifex-textured rocks which underwent rapid crystallization within ponded lobes. Characteristic associations of different rock types are interpreted in terms of variations in eruption rate, which presumably reflect proximity to the vent or major lava river. The channel-facies rocks (olivine cumulates) are flanked by sequences of spinifex-textured flow-units that formed from the episodic overflow of lava from the distributary channels.

Perring C S, Barnes S J & Hill R T 1995 The physical volcanology of Archaean komatiite sequences from Forrestania, Southern Cross Province, Western Australia. *Lithos* 34:189-207.

The geochemistry of the Perseverance and neighbouring Rocky's Reward nickel deposits, which are associated with metamorphosed komatiite flows erupted onto a substrate of felsic crystal tufts, is described by an international collaboration of researchers from CSIRO (Perth), the University of Alabama, and the University of Melbourne. The deposits are overlain by the Perseverance Ultramafic Complex, which consists of a central dunite lens flanked by olivine orthocumulates and spinifex-textured komatiites. Samples from the A-zones of komatiite flows fall into two distinct geochemical groups. Samples from flows flanking the central dunite show well-constrained linear trends of major and trace elements typical of komatiite suites related by simple olivine fractionation. Samples from the Perseverance

mine, Rocky's Reward and from unmineralized flows at the base of the Perseverance Ultramafic Complex all show evidence for light REE enrichment relative to the other group. Geochemical computer modelling suggests that the mineralization is due to wholesale assimilation of floor rocks close to the site of sulphide accumulation.

Barnes S J, Leshner C M & Keays R R 1995 Geochemistry of mineralised and barren komatiites from the Perseverance nickel deposit, Western Australia. *Lithos* 34:209-234.

Rock magentic properties and palaeomagnetism of weakly metamorphosed banded iron-formation (BIF) from the Palaeoproterozoic Hamersley Group and Proterozoic BIF-derived iron ores were investigated by P Schmidt and D Clark (CSIRO, North Ryde). Palaeomagnetic pole positions were calculated for BIFs at Paraburdoo (40.9°S, 218.9°E) and Wittenoom (36.4°S, 218.9°E) and for Mt Tom Price iron ore (37.4°S, 220.3°E) and Paraburdoo iron ore (36.4°S, 209.9°E). These poles are indistinguishable from each other, and from the Mt Jope Volcanics overprint pole. The magnetization of the BIFs was probably acquired during burial metamorphism of the Hamersley Group.

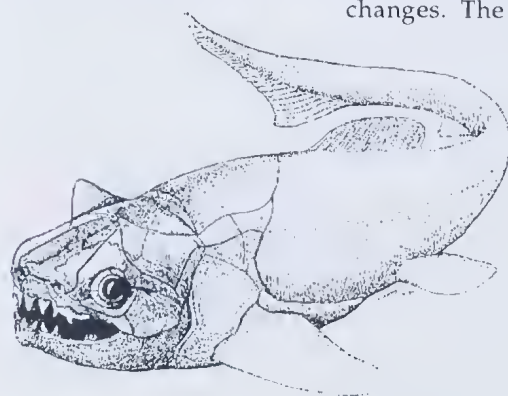
Schmidt P W & Clark D A 1994 Palaeomagnetism and magnetic anisotropy of Proterozoic banded-iron formations and iron ores of the hamersley basin, Western Australia. *Precambrian Research* 69:133-135.

Solid bitumen envelopes in Permian sandstones from the Kennedy Group are shown by B Rasmussen and J Glover (University of Western Australia) to be useful in subdividing the diagenetic sequence into three intervals, thus establishing the order of appearance of diagenetic minerals with greater precision than was previously possible. The envelopes develop from the polymerization of hydrocarbons around the radioactive detritals monazite, xenotime and zircon. Their paper reports the presence of authigenic florencite (Ce, La, Al phosphate) and xenotime (YPO₄), and bitumen-filled fission tracks in monazite for the first time in Australian sedimentary rocks.

Rasmussen B & Glover J E 1994 Diagenesis of low-mobility elements (Ti, REEs, Th) and solid bitumen envelopes in Permian Kennedy Group sandstone, Western Australia. *Journal of Sedimentary Research* A64:572-583.

Life Sciences

This most recent book published by John Long, of the Western Australian Museum, entitled 'The Rise of Fishes', provides a superbly illustrated history of the evolution of the fishes. It integrates aspects of geology, evolution, anatomy, and global environmental changes. The book is the first



complete account of the spectacular fossil history of the fishes over their 500 million year record, and provides a thorough discussion of the latest evidence for the evolution of the first fishes from invertebrates. Included in the book are hundreds of colour photographs and dramatic full-colour reconstructions of extinct fishes.

Long J A 1995 *The Rise of Fishes. 500 Million Years of Evolution*. Johns Hopkins University Press, Baltimore/University of New South Wales Press, Sydney.

This monograph by D Bickel examines all 253 species (with 208 newly described) of dipteran flies of the subfamily Sciapodinae. It describes aspects of morphology, fossil history, systematics, natural history, biogeography and accidental introductions, and systematics. It reviews all zoogeographic regions although it emphasises Australia and the Orient. Nine new genera are erected, and there are nomenclatural changes for taxa from all biogeographic regions.

Bickel D J 1995 *The Australian Sciapodinae (Diptera: Dolichopodidae)*, with a review of the Oriental and Australasian faunas, and a world conspectus of the subfamily. Records of the Australian Museum. Supplement 21.

Patterns of morphological diversity are examined by J Clements (University of Western Australia) and W Cowling (Department of Agriculture, WA) for 157 accessions of wild lupins *Lupinus angustifolius* from the Aegean region. Two groups with desirable agronomic characteristics originated in the Dodekanisos Islands; these had rapid and tall growth, prolific podding on the main stem, pods high off the ground, many upper lateral branches, large leaves, pods and seeds, and high seed yield.

Clements J C & Cowling W A 1994 Patterns of morphological diversity in relation to geographical origins of wild *Lupinus angustifolius* from the Aegean region. Genetic Resources and Crop Education 41:109-122.

Researchers from Murdoch University and the Department of Lands, Parks and Wildlife (Hobart) demonstrate a substantial correlation between the breeding ages of short-tailed shearwaters in pair bonds. This is largely explained by the prolonged pair-bond between mates and the predominant availability of unpaired, inexperienced birds. The probability of breeding success depends on the breeding ages of the partners and especially the length of their pair bond.

Bradley J S, Wooller R D & Skira I J 1995 The relationship of pair-bond formation and duration to reproductive success in short-tailed shearwaters *Puffinus tenuirostris*. Journal of Animal Ecology 64:31-38.

A survey of the Cenozoic fossil fauna of Barrow Island in northwestern Australia, by K McNamara and G Kendrick (Western Australian Museum), has yielded a rich fauna of Middle Miocene and Late Pleistocene molluscs, and Middle Miocene echinoid echinoderms. These faunas have little in common with the contemporaneous faunas from the Nullarbor Limestone in the Eucla Basin; the echinoid fauna has more in common with Miocene faunas of Java and India. The mollusc and echinoid faunas show strong affinities with modern communities.

McNamara K J & Kendrick G W 1994 Cenozoic molluscs and echinoids of Barrow Island, Western Australia. Records of the Western Australian Museum. Supplement 51.

The traditional and current uses of the genus *Eremophila*, Australian desert shrubs, have been reviewed by G Richmond (Curtin University) and E Ghisalberti (University of Western Australia). This ecologically-important genus is represented by over 200 species, of which 75% occur in Western Australia. Species of *Eremophila* have long been of cultural importance to the Aboriginal people. They are useful in revegetation programmes and have potential in horticulture and as sources of phytochemicals.

Richmond G S & Ghisalberti E L 1994 The Australian desert shrub *Eremophila* (Myoporaceae): medicinal, cultural, horticultural and phytochemical uses. Economic Botany 48:35-59.

Exposure of dormant seed to cold smoke, derived from burnt native vegetation, has a positive influence on germination in 45 of 94 species of native vegetation examined by researchers from Kings Park and Botanic Garden, and the University of Western Australia. Some species showed earlier germination if smoke-treated, whereas other species continued to germinate for a longer period of time if smoke-treated.

Dixon K W, Roche S & Pate J S 1995 The promotive effect of smoke derived from burnt native vegetation on seed germination of Western Australian plants. Oecologia 101:185-192

Researchers from the University of Western Australia have shown that the lesser long-eared bat *Nyctophilus geoffroyi* was attracted to both calling tettigoniid bushcrickets and synthesised tettigoniid calls broadcast through loud-speakers. More bats were attracted to long-duration than short-duration calls, whereas high calling rate or high calling intensity had no special attraction. Two-speaker choruses appeared to be more attractive than single-speaker choruses. These results are interpreted in the context of predation being a selective force on calling strategies of tettigoniid bushcrickets.

Hosken D J, Bailey W J, O'Shea J E & Roberts J R 1994 Localisation of insect calls by the bat *Nyctophilus geoffroyi* (Chiroptera: Vespertilionidae): a laboratory study. Australian Journal of Zoology 42:177-184.

B Lamont and E Witkowski provide a stage-by-stage protocol for identifying simple or biased lottery, or non-lottery, patterns of seedling recruitment. For four co-occurring species of Banksias after two experimental fires, seedlings still alive after 3 years of two (*Banksia speciosa* and *B. Baxteri*) conformed to a biased lottery whereas two (*B. coccinea* and *B. pulchella*) has no mathematical structure.

Lamont B B & Witkowski E T F 1995 A test for lottery recruitment among four *Banksia* species based on their demography and biological attributes. Oecologia 101:299-308.

Physical Sciences

A group of researchers from the Chemistry Department at the University of WA and the Research School of Chemistry at the ANU in Canberra have made a detailed study of the synthesis and structure of bicyclic hexamine ligands, which can act as cages for metal ions. These ligands are very strong bases, accepting up to five protons with pK_a 's ranging from 0 to 12.

Bottomley G A, Clark I J, Creaser I I, Engelhardt L M, Geve R J, Hagen Ks, Harrowfield J M, Lawrance G A, Lay P A, Sargeson A M, See A J, Skelton B W, White A H & Wilner F R 1994 The synthesis and structure of encapsulating ligands:

properties of bicyclic hexamines. *Australian Journal of Chemistry* 47:143-179.

Electrical conductivities of simple electrolytes dissolved in 2-cyanopyridine have been measured by GT Hefter (Murdoch University) and M Salomon (US Army Power Sources Laboratory). Only weak association occurs in dilute solution because of the very high dielectric constant. A conductivity maximum is observed in the very concentrated solutions typical of nonaqueous batteries.

Hefter GT & Salomon M 1994 Conductivities of 1:1 salts in 2-cyanopyridine. *Journal of Solution Chemistry* 23:579-593.

Researchers at Murdoch University have made a quantum mechanical study of the effect of excess charge on bond strengths in silane molecules. The calculations show that both positive and negative charges reduce the bond strengths so that they can be broken even by infrared light. This effect may explain the well-known photo-degradation of amorphous silicon solar cells.

Clare BW, Talukder G, Jennings PJ, Cornish JCL & Hefter GT 1994 Effect of charge on bond strength in hydrogenated amorphous silicon. *Journal of Computational Chemistry* 15:644-652.

Chemists at Murdoch University have been able to synthesize asymmetric di-acetate derivatives of benzo [c] pyrans using titanium tetraisopropoxide. These compounds are related to aphid pigments.

Giles RGF & Joll CA 1995 An asymmetric synthesis of benzo [c] pyrans related to the aphid pigments. *Tetrahedron Letters* 36:1125-1126.

Note from the Hon Editor: This column helps to link the various disciplines and inform others of the broad spectrum of achievements of WA scientists (or others writing about WA). Contributions to "Recent Advances in Science in Western Australia" are welcome, and may include papers that have caught your attention or that you believe may interest other scientists in Western Australia and abroad. They are usually papers in refereed journals, or books, chapters and reviews. Abstracts from conference proceedings will not be accepted. Please submit either a reprint of the paper, or a short (2-3 sentences) summary of a recent paper together with a copy of the authors' names and addresses, to the Hon Editor or a member of the Publications Committee: Dr S D Hopper (Life Sciences), Dr A E Cockbain (Earth Sciences), and Assoc Prof G Hefter (Physical Sciences). Final choice of articles is at the discretion of the Hon Editor.

"Letters to the Editor" concerning scientific issues of relevance to this journal are also published, at the discretion of the Hon Editor. Please submit a word processing disk with letters, and suggest potential reviewers or respondents to your letter. P C Withers, *Hon Editor, Journal of the Royal Society of Western Australia*.

The value of macroinvertebrate assemblages for determining priorities in wetland rehabilitation: A case study from Lake Toolibin, Western Australia.

R G Doupé¹ & P Horwitz

Department of Environmental Management,
Edith Cowan University, Joondalup Drive, Joondalup WA 6027

¹Present Address: PO Box 101, Kununurra WA 6743

Received June 1994, accepted April 1995

Abstract

The use of macroinvertebrates in environmental assessment is well known, but is often perceived as costly and time-consuming. Using preliminary macroinvertebrate and associated salinity data recorded at Lake Toolibin and adjacent wetlands, we discuss the salinization process and how observed faunal assemblages might be used to assess a rehabilitation program. Ninety taxa were collected from two sampling occasions, most of them being saline-tolerant forms representing widespread groups with high dispersive powers. Predominantly freshwater forms not found, but expected to occur, can be used as indicator taxa for recovery. In addition to the need for regular monitoring of the fauna, we argue for a greater emphasis on ensuring the recovery of Lake Walbyring, which contained a demonstrably different suite of macroinvertebrates.

Introduction

Lake Toolibin, approximately 200km south-east of Perth, lies at the head of a series of seasonal or ephemeral lakes which form the headwaters of the Arthur River, a tributary of the Blackwood River in south-western Australia. The clearing of native vegetation has resulted in both a rise in saline groundwater levels and an increase in saline surface run-off into the headwaters of the Arthur River (Halse 1988). Most wetlands of the system, and other parts of the Western Australian wheatbelt, have been severely affected by secondary salinization. However, Lake Toolibin has remained comparatively fresh.

Lake Toolibin Nature Reserve is a registered "Wetland of International Importance" under the Ramsar Convention. It has important conservation value as a breeding habitat for native waterfowl, including rare species (Halse 1987), and because of the occurrence of restricted vegetation types (Froend *et al.* 1987). The Department of Conservation and Land Management of Western Australia and the local Lake Toolibin Catchment Committee are engaged in tree planting and overland flow interception and diversion operations in the Lake Toolibin catchment in an effort to prevent any further decline of this Reserve. Recent efforts to monitor these restorative activities include the work of Bell & Froend (1990), who recorded the decline and mortality of wetland trees at Lake Toolibin over a five year period. The recovery plan for Lake Toolibin (Anon. 1992)

suggested that aquatic invertebrate surveys should be undertaken to provide a measure of water quality, and to indicate whether recovery criteria were being met.

Faunal composition should show a rapid response to changing wetland conditions because many macroinvertebrate taxa possess a mobile phase in their life cycle, hence they can colonize suitable habitats rapidly. In the case of Lake Toolibin, the hypothesis is that water salinity will largely dictate the type of fauna that will be found. While the "coarse relationship" (*sensu* Williams *et al.* 1990) between salinity and faunal composition is unquestionable, the role of salinization in shaping aquatic communities remains poorly understood (De Deckker 1983). The work of Williams *et al.* (1991) suggested that Australian macroinvertebrates are more tolerant to salinity than previously thought, although an alternative explanation is that only euryhaline forms persist from a once more diverse fauna.

At Lake Toolibin, neither the structure of aquatic invertebrate communities, nor the possible effects of increasing salinity on them, have been described. Baseline data are therefore necessary if we are to understand what is happening in this wetland. If macroinvertebrate assemblages are to be used as indicators for monitoring restorative change, then ideally sampling should be simple to perform (perhaps by relatively untrained people), and yield results upon which rehabilitation endpoints can be determined.

The aim of this paper is to provide a preliminary assessment of macroinvertebrate data for Lake Toolibin and adjacent wetlands as the basis for monitoring a rehabilitation programme.

Lake Toolibin Case Studies

The Lake Toolibin district had a higher than average rainfall (404 mm *cf* 358 mm) in 1992. In late September of that year, students and staff from Edith Cowan University (Joondalup) visited six sites, covering each of three major water bodies and the major habitats in the Toolibin district (Fig 1).

Water conductivity (in mS cm^{-1}) was measured at each site using a Wissenschaftlich-Technische Werkstätten conductivity meter. The measurements were converted to parts per thousand (ppt) by multiplying the value by 0.6, following Williams (1966), in order to provide comparative data to Halse (1987).

At each sampling site, recognizably different microhabitats were sampled for macroinvertebrates using a standard Freshwater Biological Association net of 500 μ mesh size. The sampling technique involved vigorously sweeping the water column from water surface to sediments over an area of approximately one square metre. Material collected was then live-picked, with representatives of morphospecies being preserved in 70% alcohol for later identification in the laboratory. A drift net (DN) with an opening of 300 mm $\times$ 330 mm and mesh size of 500 μ m was set for 24 hours in the Arthur River (upstream from site 1) to collect macroinvertebrates. Material collected (approximately 2 litres of invertebrates) was mixed and halved to reduce sample size, then preserved in 5% formalin and subsequently sorted in the laboratory. Zooplankton was sampled at each site by towing a 63 μ m mesh size zooplankton net for 5 m in approximately 0.3 m of water near the shore. Material collected was preserved in 5% formalin and subsequently sorted in the laboratory. All collections of invertebrates were identified to species level wherever possible, with adults and larvae being treated as separate taxa.

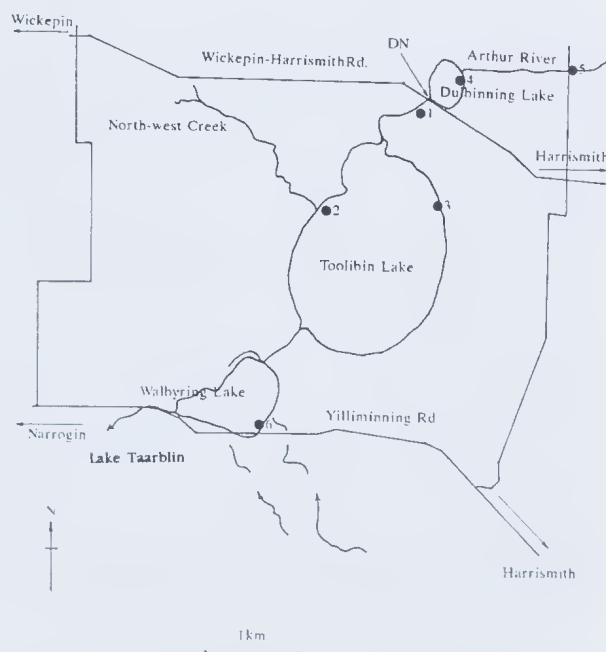


Figure 1. Location of study sites in the Lake Toolibin district showing major roads and principle drainage lines.

To examine seasonal changes and the effects of evapo-concentration, the sites were revisited by RGD in mid April 1993. Only Lake Walbyring (site 6) was resampled as before, as the other sites were dry.

Table 1 summarizes the salinity, species richness and the number of species found exclusively at each site (*i.e.* site-specific species). During the September sampling, Lake Toolibin and the three upstream sites had a salinity of 2.4-4.4 ppt, which is about one-tenth that of seawater. At this time, the salinity at Lake Walbyring was less than half the concentration found at other sites, and was the only site with "fresh" waters (where fresh might be regarded as <1.6 ppt after converting the salinity boundaries provided by Semeniuk, 1987). Whereas other sites became dry and salt encrusted over summer, Lake Walbyring in April 1993 still had a salinity below that of Lake Toolibin when it was full in September 1992.

Table 1.

Salinity and macroinvertebrate species richness at Toolibin district lake sites.

Site	Location	Salinity mS cm^{-1} (ppt)	Species Richness	Site-Specific Species
1	Arthur River	5.8 (3.5)	33	8
DN	Drift net	(see above)	29	6
2	Lake Toolibin (Western side)	5.0 (3.0)	25	2
3	Lake Toolibin (Eastern side)	4.0 (2.4)	26	3
4	Lake Dulbinning	5.8 (3.5)	31	6
5	Shallow marsh area	7.3 (4.4)	20	3
6	Lake Walbyring	1.7 (1.0)	31	14
6 ^a	Lake Walbyring	2.6 (1.6)	27	0

^a indicates April 1993 data.

A total of 90 macroinvertebrate taxa (82 of which were found in the September 1992 samples, and 27 in the 1993 sample) were recorded from the study (Appendix 1). Most of the major inland aquatic orders of invertebrates were represented. Some notable absences from the aquatic fauna were the mayflies (Ephemeroptera) and stoneflies (Plecoptera). These groups are among the insect orders thought to be sensitive to salinity levels greater than about 1.0 ppt (Hart *et al.* 1991). Lake Walbyring contained substantially more site-specific species than any other site (Table 1).

Discussion

Degradation of Lake Taarblin, immediately downstream of Lake Walbyring, became obvious in the 1930s when the death of wetland trees was thought to be due to the rise in water levels (Anon. 1987). According to Sanders (1991), salinization of Lake Taarblin was thought to have begun in the late 1950s, with Lakes Toolibin, Dulbinning and Walbyring following a similar pattern in the 1960s. Along with this historical pattern is a seasonal variability in salinity with lake waters becoming more saline as they become shallower (through evapoconcentration), and a tendency for salinities to vary interannually, presumably as a result of annual

rainfall variations and the occasional flushing of salt when lakes overflow (Halse 1987).

We know that the rainfall received in 1992 was above average and that the lakes of the Toolibin district contained water for longer than normal. Similarly, September sampling reflects wetter conditions and lower salinities compared to other times of the year. For both these reasons, our data should represent the "fresher" end of the values collected recently for these wetlands. However, historical depth and salinity data of Lakes Toolibin and Walbyring collected by the Department of Conservation and Land Management (JAK Lane, unpub. data) show the reverse pattern. Salinities for Lake Toolibin were higher in 1992 than they were in 1983 or 1990, the two other years in which the lake was full of water. Over this period, Lake Walbyring was consistently fresher than Lake Toolibin, and does not seem to have had as strong a trend toward salinization, as we also found.

The hydrology and hydrogeology of the Toolibin area is complex; however, Lake Walbyring does appear anomalous, with comparatively fresher waters than the other lakes, when full. Lake Toolibin is thought to be a groundwater recharge area, where waters enter a shallow, saline aquifer beneath the lake. Stokes & Sheridan (1985) believe these waters realize superficial expressions at Lake Walbyring and the severely salt-scalded Lake Taarblin, with Lake Walbyring receiving overflow from Lake Toolibin at over bank-full stage. It is unclear how the waters of Lake Walbyring are being maintained, especially in its comparatively freshwater state. Perhaps the lacustrine deposits are creating a "perched" effect, and/or this waterbody receives run-off from part(s) of a catchment that are less salt-affected than those drainage lines which supply other wetlands of the system.

The aquatic macroinvertebrate taxa found at Lake Toolibin and adjacent wetlands are predominantly euryhaline forms typical of brackish/slightly saline habitats, and most have wide dispersive powers. The relative dissimilarity of the Lake Walbyring fauna may imply that this wetland has retained fresher elements otherwise lost due to the salinization of the Lake Toolibin area. Alternatively, faunal assemblages may be seasonally opportunistic with respect to salinities. In wetlands that experience fluctuations in salinity, there may be a succession of species as salinities change. For instance, unpublished data (S Halse, *pers. comm.*) taken at Lake Walbyring in September 1985 and August 1986 (when salinities were far greater) show a fauna much more tolerant of saline conditions; 28 taxa were found on these two sampling occasions, yet no more than one third of these taxa were found by us at Lake Walbyring. No Ephemeroptera or Plecoptera, were found in any collections.

As with many biological surveys, our interpretation of the data is based on a "snapshot" sampling regime, and some caution is required. Nevertheless, the magnitude of the differences between the fauna of Lake Walbyring and Lake Toolibin, apparently related to differences in salinity, suggest that a single macroinvertebrate collection by relatively untrained, but supervised personnel, can yield valuable baseline data. Any remaining ambiguities, like those discussed above, could be resolved best through the longer term monitoring and detailed analyses

of macroinvertebrate assemblages. Monitoring over time would be required to document the full range and seasonality of species, and determine whether a more regional, less cosmopolitan fauna becomes established as tree-planting and hydrological manipulations have effect.

We propose that the faunal characteristics at Lake Walbyring found in September 1992 could be the minimum required to indicate successful rehabilitation if consistently found at Lake Toolibin; other fauna like mayflies (Ephemeroptera) could also be indicators of wetland recovery from saline effects. Furthermore, the fresher waters of Lake Walbyring are a habitat for potentially re-colonizing species and should be monitored.

The production of these preliminary findings are timely, given that decisions regarding water and salinity management at Lake Toolibin are imminent. Engineering solutions, including water diversion measures, may be the only short-term method of saving Lake Toolibin, yet our results indicate that in a wetland chain, one lake cannot be treated in isolation from neighbouring wetlands, and that a greater understanding of catchment conditions at least at Lake Walbyring, is required. Decisions about rehabilitating Lake Toolibin should not exclude the value of Lake Walbyring or any other regional wetland which may, at one time or another, harbour an assemblage of freshwater species.

Acknowledgements: Permits to conduct the study were provided by the Department of Conservation and Land Management. The following are thanked for their contributions to this paper: the students from Edith Cowan University (Water and Wetlands Management unit, 1992); Darren and Fiona Ryder for their initial sorting of 1992 samples; Mr Kim Richardson for assistance with sampling and with identifications. Drs Mark Harvey, Don Edward and the late Shirley Balla, Mrs Shirley Slack-Smith, Ms Faye Cheal and Ms Sue Harrington identified species. Rainfall information was supplied by the Western Australian Bureau of Meteorology. Mr Jim Lane and Dr Stuart Halse (CALM) allowed us to use and cite unpublished data. Dr Halse also suggested the work be done, and kindly provided a critique of an earlier draft of this manuscript.

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Appendix 1.

Invertebrate taxa found in the Northern Arthur River wetlands. (For explanation of site codes, see Table 1 and Figure 1).

PHYLUM CLASS (ORDER) Family	Species	1	DN*	2	Site		3	4	5	6	6 ^a
PLATYHELMINTHES	Sp	X								X	
NEMATODA	Sp	X									X
ANNELIDA OLIGOCHAETA	Sp1 Sp2 Sp3	X								X	X
HIRUDINEA	Sp	X					X		X		X
ARTHROPODA ARACHNIDA (ACARINE)	<i>Eylais</i> sp <i>Linnesia</i> sp		X							X	
(ARANEAE)	<i>Singotypa</i> sp									X	
Tetragnathidae	<i>Tetragnatha</i> sp									X	X
CRUSTACEA (NOTOSTRACA)	<i>Lepidurus apus viridis</i> Baird								X		
(CLADOCERA)											
Chydoridae	<i>Pleuroxus</i> sp	X		X		X					
Daphniidae	<i>Ceriodaphnia</i> sp <i>Daphnia carinata</i> King <i>Simocephalus</i> sp	X X X	X X X	X X X		X X X		X X X	X X X	X X X	X X X
Macrothricidae	<i>Echinisca</i> sp <i>Macrothrix ?breviseta</i> Smirnov	X X		X X		X X		X X	X X		X X
Moinidae	Sp	X	X			X				X	X
(OSTRACODA)											
Cypridacea	<i>Cyprinotus ?edwardi</i> McKenzie <i>Diacypis spinosa</i> De Deckker <i>Mytilocypris ?ambigua</i> De Deckker <i>Mytilocypris</i> sp 2 <i>Alboa worooa</i> De Deckker <i>Bennelongia</i> sp <i>Sarscypridopsis aculeata</i> (Costa)	X X X X X X X	X X X X X X X	X X X X X X X		X X X X X X X		X X X X X X X		X X X X X X X	
(CHONCHOSTRACA)	<i>Cyzicus</i> sp	X									
(COPEPODA - Calanoida)											
Centropagidae	<i>?Calamoecia</i> sp	X	X	X						X	X
(COPEPODA - Cyclopoida)	<i>?Microcyclops</i> sp	X		X				X	X	X	
(AMPHIPODA)											
Ceinidae	<i>Austrochiltonia</i> sp	X	X	X		X		X	X	X	
(DECAPODA)											
Palaemonidae	<i>"Palaemonetes australis"</i> Dakin	X						X	X		
Parastacidae	Claw of <i>Cherax albidus</i> Clark	X									
INSECTA											
(ODONATA - Anisoptera)											
Aeshnidae	<i>Hemianax papuensis</i> (Burmeister)									X	X
(ODONATA - Zygoptera)											
Coenagruidae	<i>Xanthagrion erythroneurum</i> (Selys)									X	
Lestidae	<i>Austrolestes annulosus</i> (Selys) <i>Austrolestes io</i> (Selys)									X X	X X
(HEMIPTERA)											
Corixidae	<i>?Agraptocorixa</i> sp <i>Micronecta</i> sp1 <i>Micronecta</i> sp2										X X X

Appendix 1 (continued)

PHYLUM		Site							
CLASS (ORDER)									
Family	Species	1	DN*	2	3	4	5	6	6 ^a
Notonectidae	<i>Sigara</i> sp		X	X		X		X	
	Sp5								X
	<i>Anisops</i> sp1		X	X	X			X	X
	<i>Anisops</i> sp2							X	X
	<i>Paranisops</i> sp	X		X		X		X	X
	Sp4		X			X		X	
(DIPTERA)									
Chironomidae	<i>Chironomus aff. alternans</i> Walker					X			X
	<i>Chironomus tepperi</i> Skuse	X	X	X	X	X	X		
	<i>Cryptochironomus griseidorsum</i> Kieffer				X				
	<i>Dicrotendipes conjunctus</i> Walker					X			
	<i>Kiefferulus intertinctus</i> Skuse								X
	<i>Procladius paludicola</i> Skuse		X			X	X		X
	<i>Procladius villosimanus</i> Kieffer					X			
Ephydriidae	Sp			X					
Ceratopogonidae	Sp							X	
Culicidae	<i>Anopheles (Cellia)</i> sp					X			
	<i>Culex</i> sp1							X	
Tabanidae	<i>Culex</i> sp2			X					
	Sp							X	
Unidentified Dipteran Pupae	Sp1		X	X	X	X			X
	Sp2							X	
	Sp3			X					X
(TRICHOPTERA)									
Leptoceridae	<i>Triplectides australis</i> Navas								X
(COLEOPTERA)									
Dytiscidae (larvae)	<i>Antiporus</i> sp	X	X	X	X	X	X		
	<i>Bidessus</i> sp1		X		X				
	<i>Bidessus</i> sp2				X				
	<i>Homeodytes scutellaris</i> (Germar)		X						
	<i>Hydaticus</i> sp1	X	X	X		X		X	
	? <i>Hydaticus</i> sp2	X		X	X				
	<i>Hydrovatus</i> sp	X							
	<i>Laccophilus</i> sp1			X	X				
	<i>Lancetes lanceolatus</i> (Clark)		X						
	<i>Macroporus</i> sp1				X	X	X		
	<i>Macroporus</i> sp2						X		
	<i>Necterosoma</i> sp				X				
	<i>Paroster</i> sp		X		X		X		
	? <i>Rhantaticus</i> sp1				X				
	? <i>Rhantaticus</i> sp2	X							
	<i>Allodesus</i> sp	X	X	X	X	X	X	X	X
	<i>Australphilus montanus</i> Watts	X	X		X	X	X	X	
	<i>Copelatus</i> sp							X	
	<i>Laccophilus</i> sp2	X	X						X
	<i>Berosus</i> sp1					X	X		
	<i>Berosus</i> sp2								X
	<i>Laccobius</i> sp		X						
	<i>Berosus</i> sp3		X						
(adults)	Sp							X	
Curculionidae (adult)	Sp								
Haliplidae (adult)	<i>Haliplus</i> sp	X							
Hygrobiidae (adult)	<i>Hygrobia australasiae</i> (Clark)			X	X	X		X	
Noteridae (adult)	Sp	X							
(LEPIDOPTERA)									
Pyalidae (larvae)	Sp		X						
MOLLUSCA									
GASTROPODA									
(PULMONATA)									
Planorbidae	<i>Physastra</i> sp								X
Species Richness (by site)		33	29	25	26	31	20	31	27
Total Species Richness (all sites): 90 species									

* Drift Net

^a site 6 sampled in autumn.

An Upper Cretaceous chert nodule, apparently marine ballast, from Princess Royal Harbour, Western Australia

J E Glover¹, R J Davey² & C E Dortch³

¹Department of Geology and Geophysics, University of Western Australia, Nedlands WA 6907

²Simon Petroleum Technology Ltd Exploration Services, Llandudno, Gwynedd LL30 1SA, United Kingdom

³Anthropology Department, Western Australian Museum, Francis Street, Perth WA 6000

Manuscript received December 1994, accepted March 1995

Abstract

A stone nodule recovered in the excavation of a silo foundation in the Port Authority area of Princess Royal Harbour, Western Australia, is composed of Upper Cretaceous chert, a lithological type anomalous to the region. The chert in this nodule closely resembles black English flint, and contains algal microfossils (dinoflagellates) that are more likely to be European than Australian. The specimen is, almost certainly, a nineteenth century ballast stone from northwestern Europe, and may have come from Thames River gravels or similar deposits in southern England. The investigation shows the danger of making uncritical assumptions about the origin and provenance of chert objects in southwestern Australia.

Introduction

In 1968, Mr Brian Ayre of Rockingham, W.A., picked a nodule of flint (generally classified by geologists as chert) from the lower part of a six metre-deep silo foundation in the Port Authority area of Princess Royal Harbour, at Albany (35° 03' S 117° 54' E) on the southern coast of Western Australia (see Fig 1). He observed that the foundation walls consisted of layers of beach sand, marine shell grit, a 60 cm-thick zone of black mud, and two or more layers of whole marine shells (*pers. comm.*). The stone came from the disturbed floor of the foundation. Mr Ayre passed the specimen to the Western Australian Museum in 1993 for identification. On the basis of superficial examination, the stone was tentatively identified as a naturally flaked chert or flint nodule from England or elsewhere in northwestern Europe. The occurrence of a putative ballast stone at a depth of about six metres can be explained by the massive dredging and earth-filling operations done in the Albany Port Authority area around the turn of the century (Garden 1978), several decades after sailing ships first could have dumped loads of English or European chert ballast in Princess Royal Harbour. Although we have not been able to verify the dumping of flint ballast in Princess Royal Harbour, it is reasonable to assume that the practice took place during the half century or more (ending about 1900) when sailing ships arriving from England were loading cargos (Garden 1978). It is also possible that the nodule came from a nearby wreck.



Figure 1. Map of southwestern Australia showing the distribution of the Plantagenet Group, and localities mentioned in the text.

Results

General description

The object is irregularly shaped and measured roughly 11.5 X 7 X 6 cm (Fig 2) and weighed 461.8 gm before the removal of cores in the laboratory. It is a flint (or chert) nodule that is randomly flaked and rolled on several parts. The angles between some of the large flake scars and adjacent striking platforms are much more obtuse than normally associated with, or even possible by, knapping (*i.e.* artificial flaking), but are like those seen on pebbles flaked by wave action. Consistent with this is the rolled condition of the piece, *i.e.* it has heavy abrasion and multiple chipping (tiny negative flake scars) extending along the ridges formed between the various flake scars. The flaking appears to have been done by wave action in which the nodule would have been flung and dragged against other nodules, as on a pebble beach (*cf.* Shackley 1974).

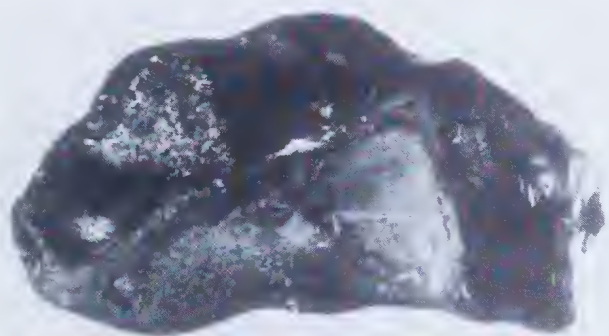


Figure 2. The Princess Royal Harbour chert nodule. Note the smooth, slightly patinated surface (bottom centre and bottom left) and the shiny black conchoidal fracture (right and top centre). Length of specimen = 11.5 cm.

Petrology

The surface of the nodule is mostly rounded, but where flaked it has well-developed conchoidal fracture. The fresh rock is generally shiny black (N1) but in places it is irregularly mottled and ranges to medium light grey (N6) and greyish orange (10YR 7/4). Locally, there is a surface patination about 0.75 mm thick ranging from greyish orange (10 YR 7/4) to pale yellowish brown (10 YR 6/2) (colours based on Rock-Color Chart Committee, 1963). There is no effervescence in cold dilute hydrochloric acid, indicating the absence of calcite.

For determinative purposes, two solid cylindrical cores, one 2 x 1.5 cm and one 2 x 2.5 cm, were drilled from the specimen. The chert fractured easily and irregularly, and the objective of retaining the slightly patinated tops of the cores to restore the original appearance was only partly realised. Portions of the cores were used for thin sections, and for the extraction of palynomorphs.

The rock is composed mainly of cryptocrystalline quartz (Fig 3). In thin section, there are various dark grey-brown patches ranging from partly to highly silicified argillaceous material, which are up to three mm long.

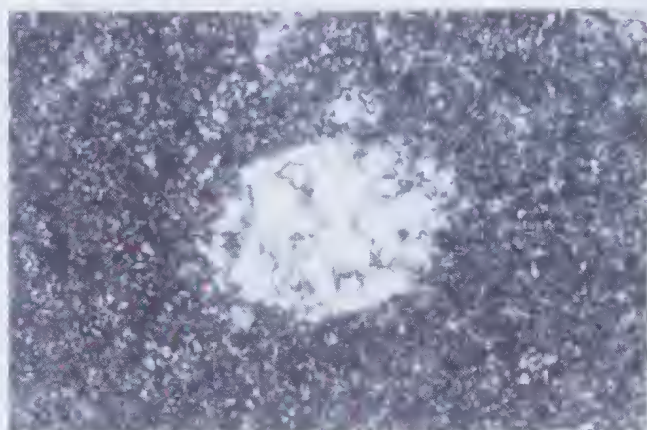


Figure 3. Typical thin-section field of Princess Royal Harbour chert nodule under crossed polarisers. The central chalcedonic mass, 0.25 mm long, may represent an in-filled fossil cavity. Remainder of field is cryptocrystalline silica.

The argillaceous areas grade fairly sharply into surrounding chert. There are also rare minute granules of hematite, possibly from the oxidation of pyrite.

Fossils are abundant. Most of the fossils are siliceous palimpsests, indeterminate except at broad taxonomic levels; they consist of foraminiferal tests, curved elongate shards that were probably shell fragments, and other debris. Spicules are abundant and may have been siliceous originally. There are some black carbonaceous flakes. The chambers of fossils are filled with cryptocrystalline quartz, radiating chalcedony, or argillaceous matter. Test walls are commonly converted to cross-fibre silica, apparently chalcedony. A remarkable feature is the presence of sparse but excellently preserved uncompressed dinoflagellate cysts that are clearly visible in thin section.

The rock is evidently a secondary chert originally consisting of a foraminiferal and spicular sediment. The excellent preservation of the dinoflagellate cysts is consistent with early post-depositional solidification caused by silicification at shallow depth. The argillaceous patches may represent intraclasts but, if so, other clasts are conspicuously absent. Alternatively, the patches may represent areas disturbed by animals burrowing in poorly consolidated calcareous ooze.

Palynology

After digestion of the silica from the core sample to concentrate the organic debris, a sparse but diverse and well-preserved assemblage of dinoflagellate cysts was recovered. The identified taxa are listed in Table 1.

Provenance and age

Dr N G Marshall and Dr A N Bint, who initially examined the palynoflora, concluded (*pers. comm.*) that it was of Late Cretaceous age and not typically Australian. They could not rule out a Northern Hemisphere origin. Detailed examination of the material has confirmed and extended these observations of Marshall and Bint. The most abundant taxon is *Spiniferites ramosus*, a long-ranging dinoflagellate cyst. The dinoflagellate association is completely consistent with a provenance in western Europe, including the United Kingdom. It should be added that

Table 1

Abundance of taxa in the palynoflora of the chert object from Princess Royal Harbour

Taxon	Proportion of palynoflora
Marine Microplankton	
<i>Acanthaulax wilsonii</i> Yun 1981	6%
acanthomorph acritarchs	1%
? <i>Actinotheca aphroditae</i> Cookson & Eisenack 1980	3%
<i>Apteodinium deflandrei</i> (Clarke & Verdier 1967) Lucas-Clark 1987	Present
<i>Atopodinium perforatum</i> (Clarke & Verdier 1967) Masure 1991	1%
<i>Cleistosphaeridium</i> spp	2%
<i>Coronifera oceanica</i> Cookson & Eisenack 1958	Present
<i>Coronifera striolata</i> (Deflandre 1937) Stover & Evitt 1978	Present
? <i>Cribroperidinium</i> sp	Present
<i>Dinopterygium cladoides</i> Deflandre 1935	1%
<i>Elytrocysta circulata</i> (Clarke & Verdier 1967) Stover & Helby 1987	4%
<i>Endoscrinium campanula</i> (Gocht 1959)	
Vozzhennikova 1967	1%
<i>Exochosphaeridium</i> spp	2%
<i>Florentinia buspina</i> (Davey & Verdier 1976) Duxbury 1980	4%
<i>Florentinia ferox</i> (Deflandre 1937) Duxbury 1980	1%
<i>Florentinia tenera</i> (Davey & Verdier 1976) Duxbury 1980	1%
<i>Heterosphaeridium</i> sp	3%
<i>Histiocysta palla</i> Davey 1969	1%
<i>Hystriochodinium pulchrum</i> Deflandre 1935	2%
<i>Hystriochosphaeridium recurvatum</i> (White 1842) Lejeune-Carpentier 1940	1%
<i>Isabelidinium cooksoniae</i> (Alberti 1959) Lentin & Williams 1977	1%
<i>Laciniadinium</i> sp	1%
<i>Odontochitina costata</i> Alberti 1961	Present
<i>Oligosphaeridium</i> complex (White 1842) Davey & Williams 1966	1%
<i>Palaeohystriochophora infusorioides</i> Deflandre 1935	1%
<i>Palambages</i> sp	Present
<i>Pterodinium cingulatum</i> (O Wetzel 1933) Below 1981	1%
<i>Sentusidinium</i> sp	6%
<i>Spinidinium echinoideum</i> (Cookson & Eisenack 1960) Lentin & Williams 1976	1%
<i>Spiniferites ramosus</i> group (Ehrenberg 1838) Mantell 1854	41%
<i>Surculosphaeridium longifurcatum</i> (Firtion 1952) Davey <i>et al.</i> 1966	1%
<i>Tanyosphaeridium</i> sp	1%
<i>Trithyrodinium</i> spp	1%
<i>Valensiella reticulata</i> (Davey 1969) Courtinat 1989	1%
<i>Valensiella</i> sp	4%
<i>Xenascus ceratioides</i> (Deflandre 1937) Lentin & Williams 1973	1%
Terrigenous pollen grains	
angiosperm pollen indeterminate	1%
bisaccate pollen undifferentiated	1%

palynological species were widely distributed during the Late Cretaceous (Costa & Davey 1992), and most of those listed here have also been recorded from Western Australia (Marshall 1975, Helby *et al.* 1987), which had comparable latitudes with western Europe during the epoch. However, there are several forms, including *Balteocysta perforata* and species of *Conosphaeridium* which occurred in the Australian region at the time but have not been observed in this assemblage. The composition of the palynoflora is therefore more European than Australian, but species variation in the Chalk Sea assemblages is too slight to show where the chert is likely to come from in western Europe.

The flint is Late Cretaceous in age, probably late Turonian to Coniacian, on the basis of significant occurrences of *Acanthaulax wilsonii* (Fig 4), *Florentinia buspina*, *F. tenera*, *Surculosphaeridium longifurcatum* and *Isabelidinium cooksoniae* (single specimen).

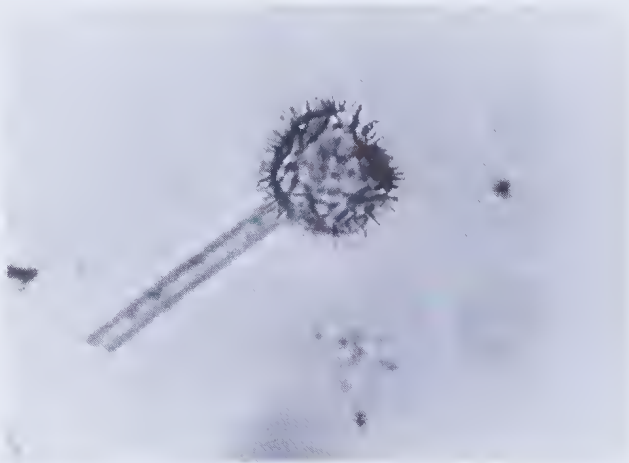


Figure 4. The resistant resting cyst of the dinoflagellate *Acanthaulax wilsonii*, which composes 6% of the total palynoflora. Width of field 0.23 mm.

Discussion

Many chert objects, overwhelmingly of Aboriginal origin, have been found on or near the surface in southwestern Australia (Glover 1984). Most are flakes, but a few larger artifacts have been found: for example the Broke Inlet biface from about 150 km west of Albany (Glover *et al.* 1993), weighed 1797 grams. The artifacts are composed of both non-fossiliferous and fossiliferous chert. Non-fossiliferous artifacts were derived from the Proterozoic Coomberdale Chert or other Precambrian units. Fossiliferous chert, on the other hand, came either from silicified Eocene rocks along west coast areas now submerged by the sea, or from silicified Eocene Plantagenet Group rocks cropping out in the south coastal region, or from silicified Plantagenet rocks now submerged off the south coast. The estimated age of the silicified rock ranges from Early to Late Eocene. No potential source of chert containing Late Cretaceous fossils in southwestern Australia is known to us.

The significance of the fossils in secondary chert should be considered briefly. Fossils give the age of the original sediment, which may be substantially greater

than that of the chert. McGowran (1989) stated that a world-wide Eocene process of silicification reached its peak in early Middle Eocene. Fortunately, the time of silicification in some cherts can be inferred from their texture. Delicate uncrushed palynomorphs in the Dunsborough biface (Glover *et al.* 1978) indicate early solidification of the rock by silicification (B Balme, *pers. comm.*). Similarly, the presence of uncompressed Late Cretaceous dinoflagellate cysts in the Upper Cretaceous chert of western Europe is consistent with a silicification depth of 5-10 metres or less, according to Clayton (1986). The excellent preservation of dinoflagellate cysts in the Princess Royal Harbour object accords with shallow silicification. In each of these examples, therefore, the fossils represent the age of the chert as well as the age of the original sediment.

Not all chert objects found in southwestern Australia are necessarily local. McCarthy (1958) implies that flint implements have more than once been dumped with ballast in Australia, and Tindale has stated that flint tools have been recovered from "Thames gravel" ballast at Port Lincoln, South Australia (see Dortch & Glover, 1983, p. 330). English flint pebbles may have been used in the processing of gold ore in the Kalgoorlie area during the 1890s according to Hutchinson (*pers. comm.*, see Dortch & Glover 1983). Charleton (1903) refers to the use of "quartz pebbles from Norway" in the Hannans Star Mill, but the term may have been a misnomer for chert. Finally, an implement of chert containing fossils of indeterminate age found near Scaddan, Western Australia (400 km ENE of Albany) is considered to be an Acheulian (*i.e.* Lower Palaeolithic) biface brought by ship from England, either as a collector's item or ballast (Dortch & Glover 1983). There were thus several ways in which exotic siliceous stone could have entered Western Australia.

What is a likely Northern Hemisphere source for the nodule from Princess Royal Harbour? According to Scott (1993), many Quaternary and Recent sand and gravel deposits in southern England are characterised by more than 80% flint of Late Cretaceous age. The chances of flint ballast in Australia having been derived from those areas are obviously significant.

The Princess Royal Harbour stone resembles black flint from western Europe. The macroscopic appearance, Late Cretaceous age and well-preserved palynomorphs, combined with the heavily rolled condition, suggest that the Princess Royal Harbour object is a naturally flaked nodule deriving from a pebble or shingle beach (or other gravel deposit) in western Europe, and more specifically from southern England. It is probably a 19th century ballast stone that was inadvertently deeply buried within the highly disturbed, made ground in the Port Authority

area. It adds to evidence that untested assumptions of Eocene age for fossiliferous chert objects in southwestern Australia should not be accepted uncritically.

Acknowledgements. Drs N G Marshall and A N Bint, of Woodside Off-shore Petroleum Pty Ltd made a preliminary examination and interpretation of the palynological material, and suggested that it be sent to one of us (RJD). Helpful discussions were had with Dr B E Balme of the Department of Geology and Geophysics, The University of Western Australia. R J Davey publishes with the approval of the Directors of Simon Petroleum Technology Ltd.

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Freshwater biogenic tufa dams in Madang Province, Papua New Guinea

WF Humphreys¹, SM Awramik² & MHP Jebb³

¹Terrestrial Invertebrate Zoology, Western Australian Museum, Francis Street, Perth, W A 6000

²Department of Geological Sciences, Preston Cloud Research Laboratory, University of California, Santa Barbara, CA 93106 USA

³The Christensen Research Institute, PO Box 105, Madang, Papua New Guinea; present address: Department of Botany, Trinity College, Dublin 2 EIRE

Manuscript received January 1995; accepted March 1995

Abstract

A large, fresh water calcareous tufa deposit occurs on a minor tributary of the lower Gogol River in Madang Province, Papua New Guinea. The tufa, apparently unique in the area, occurs just downstream of a natural river-tunnel in limestone. The river has a constant flow and is fringed by lowland rainforest. The river runs over a series of terraces formed by tufa dams and is unvegetated by macrophytes. The tufa is complex, consisting of porous, unlaminated calcite, laminated and banded stromatolites, and calcite encrusted insect tubes. Surfaces of the tufa have an epilithic community of insects, green algae, and microbes (rich in cyanobacteria and diatoms) that contributed to tufa formation. The lips of the tufa dams have a greater concentration of insect tubes, stromatolites, and filamentous green algae than elsewhere in the tufa. The associated fauna consists of caddis fly larvae (Trichoptera), midges (Chironomidae) and aquatic lepidopteran larvae (Pyrilidae). The deposit is a hybrid of real stromatolites and classical tufa. This unusual equatorial tufa deposit indicates that tube-building insects can play a major role in tufa deposit construction.

Introduction

A series of calcareous tufa dams occur downstream of a river cave in lowland rainforest in equatorial northern Papua New Guinea (Fig 1). The formation is notable because it is apparently unique within a large area and because close inspection in the field shows that it is intimately associated, *inter alia*, with a rich arthropod fauna and stromatolites. This paper describes the context, structure and components of the formation.

Tufa, a spongy, porous, terrestrial, semifriable variety of travertine (Bates & Jackson 1987), is found forming dams and terraces in a freshwater stream in Madang Province, Papua New Guinea. The formation of tufa involves the localized precipitation of calcium carbonate due to processes that range from abiogenic precipitation caused by CO₂ degassing to biotic factors such as photosynthesis that also remove CO₂ (see Pentecost 1981).

Tufa often occurs at the mouths of springs, along streams, and on the shores of lakes (Scoffin 1987, Bates & Jackson 1987). The term 'tufa' apparently has its origin from Pliny (23 to 79 AD) who used the term 'tophus' (*thophus*) for encrustations on plant remains and porous volcanic rocks (Julia 1983, Ford 1989). The term travertine is often reserved for a hard, dense variety of terrestrial calcium carbonate deposit (Bates & Jackson 1987). According to Ford (1989), tufa is more or less synonymous with travertine and he prefers tufa. Julia (1983), on the other hand, uses travertine for all freshwater calcium

carbonate encrustations. Chafetz & Folk (1984) use travertine as a general term for all freshwater carbonates around springs while Riding (1991) prefers that travertine be restricted to warm spring carbonate deposits. We follow the usage of Scoffin (1987) and Bates & Jackson (1987).

Most tufas that have been studied are from highly seasonal environments, mainly in the northern temperate and continental regions (Ford 1989). Tufas from low latitude regions, however, are locally abundant (e.g. Dunkerley 1981) and may form in seasonally arid settings like those from the Napier Range, Western Australia (Viles & Goudie 1990).

The tufa in Madang Province, Papua New Guinea, is a low latitude deposit that forms dams and terraces along a river draining a karst region (Fig 2). A complex community of aquatic insects, algae, and cyanobacteria is associated with the tufa. Unlike in many other riverine tufa deposits (e.g. Pentecost 1987), mosses and macrophytes are not evident. The internal structure of the tufa is variable and ranges from porous, unlaminated carbonate, to complex associations of calcified insect tubes and small stromatolites (with moulds of filamentous microbes). The calcified insect tubes are common in much of the tufa. The association of the complex biota with the tufa, the calcified insect tubes, the stromatolites, the preserved moulds of filamentous microbes, and the organic-rich nature of the tufa suggest that the biota play a major role in the formation of the tufa. The Madang tufa is important because tufas from tropical environments have not been studied in detail; it also indicates that

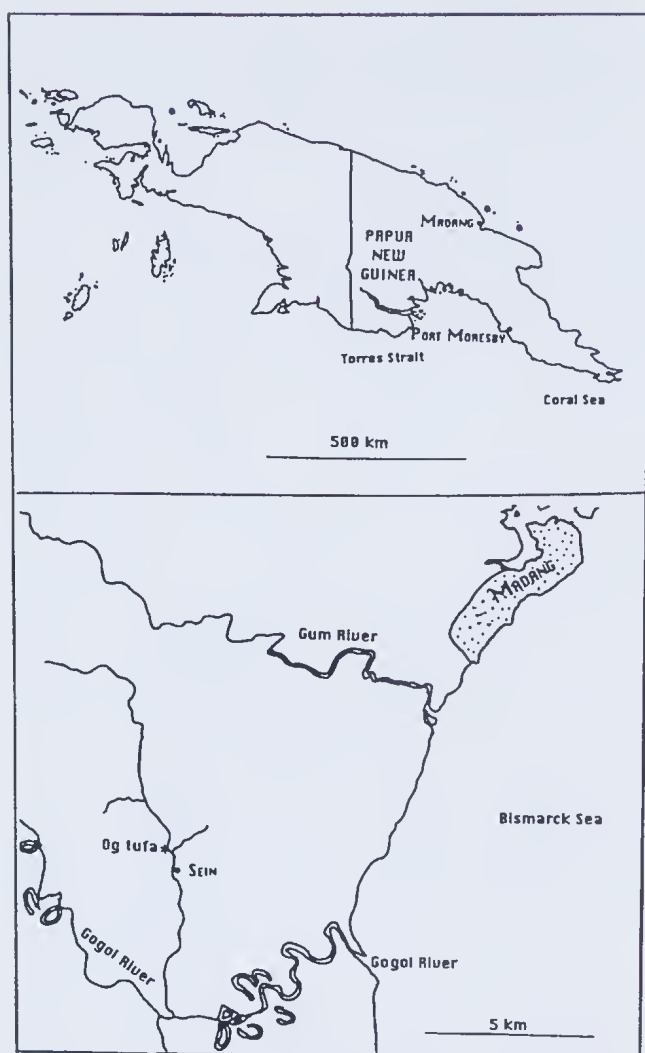


Figure 1. Location map of the Og tufa in Papua New Guinea.

tube-building insects can play a major role in tufa formation and that well-developed stromatolites occur in tufa and contributed to the carbonate buildup.

Description of the area

Location

The tufa deposit occurs in a gorge of a minor lower tributary of the Gogol River (Fig 1), downstream of the exit of a ca. 300 m long natural river-cave (the Og Cave) in the Wandokai Limestone; the river runs briefly through this natural tunnel, the remainder of its course being over ground. The locality is ca. 0.8 km northwest from Sein village, Madang Province, Papua New Guinea (5°18'S 145°43'E).

Climate

The climate is seasonal. The area comes under the influence of the north-west monsoon from December through March and the south-east trade winds for the rest of the year. The mean annual rainfall of ca. 3300 mm masks the high variability (2000-4500 mm over the last 40 years) that results from the strong impact of the El

Niño Southern Oscillation (ENSO) on this coast. The high rainfall, together with a mean monthly temperature of between 23 and 33°C support a lowland humid forest on infrequently drying soils overlain by volcanic ash (Bleeker 1983).

Geology

The Wandokai Limestone is of Pleistocene-Holocene age and forms the bedrock of the region. This limestone is a massive and crudely bedded biocalcarenite, calcarenite, calcilitite, and calcareous mudstone with subordinate lithic arenite, conglomerate, and clay (Robinson *et al.* 1976). Although there is noticeable surface drainage, the area is a cavernous karst with predominantly underground drainage.

Methods

The tufa deposit was mapped (Fig 3) to Grade 5-3 using standard speleological methods (Ellis 1976) employing a tape measure, compass, and inclinometer (Suunto). Samples of the deposit and water were collected for laboratory analyses. Some tufa pieces were fixed in neutral formalin in a local laboratory for later microbiological studies.

Samples of the fauna from a number of distinct habitats within the tufa deposit (Fig 4) were taken for identification. Organisms were also extracted from the collected tufa samples. Sweep net samples were taken during the day from the vegetation fringing the pools and collections made at night on the tufa using a black light.

In situ oxygen concentration was measured using a Hanna Instruments HI 8543 portable dissolved oxygen meter. *In situ* hydrogen ion concentration was measured using a Beckman 031 pH meter, calibrated before and after use with Labchem calibration solutions. Water temperature was measured *in situ* using the pH meter calibrated against a certified thermometer. All other measures of water chemistry were made on samples collected (both filtered and unfiltered) in triple acid-washed bottles and kept frozen for later analysis.

Ca²⁺, Mg²⁺, K⁺, and Na⁺ were analyzed by atomic absorption spectrophotometry (Varian/Spectra 30/40) and other analyses followed Strickland & Parsons (1972). X-ray powder diffraction analysis of one tufa sample (SBO305) was performed using a Philips Powder Diffractometer (12045/P3) and Random Technology controller (DFC-331 B).

Microorganisms were examined as wet mounts prepared from tufa preserved in neutral formalin. The outer surface of the tufa was scraped off and the calcite dissolved in dilute HCl. The insoluble materials were then washed with deionized water and a wet mount prepared. Samples were examined using a Zeiss Photoscope II under white light, phase contrast, and Nomarski Interference Contrast. Freshly fractured surfaces were examined under a Nikon SMZ-10 stereomicroscope to determine the extent to which larger microbes may occur below the surface.

Tufa samples were cut with a rock saw and freshly cut surfaces were examined by eye, hand lens, and a Nikon stereomicroscope. Thick (ca. 45 µm) petrological

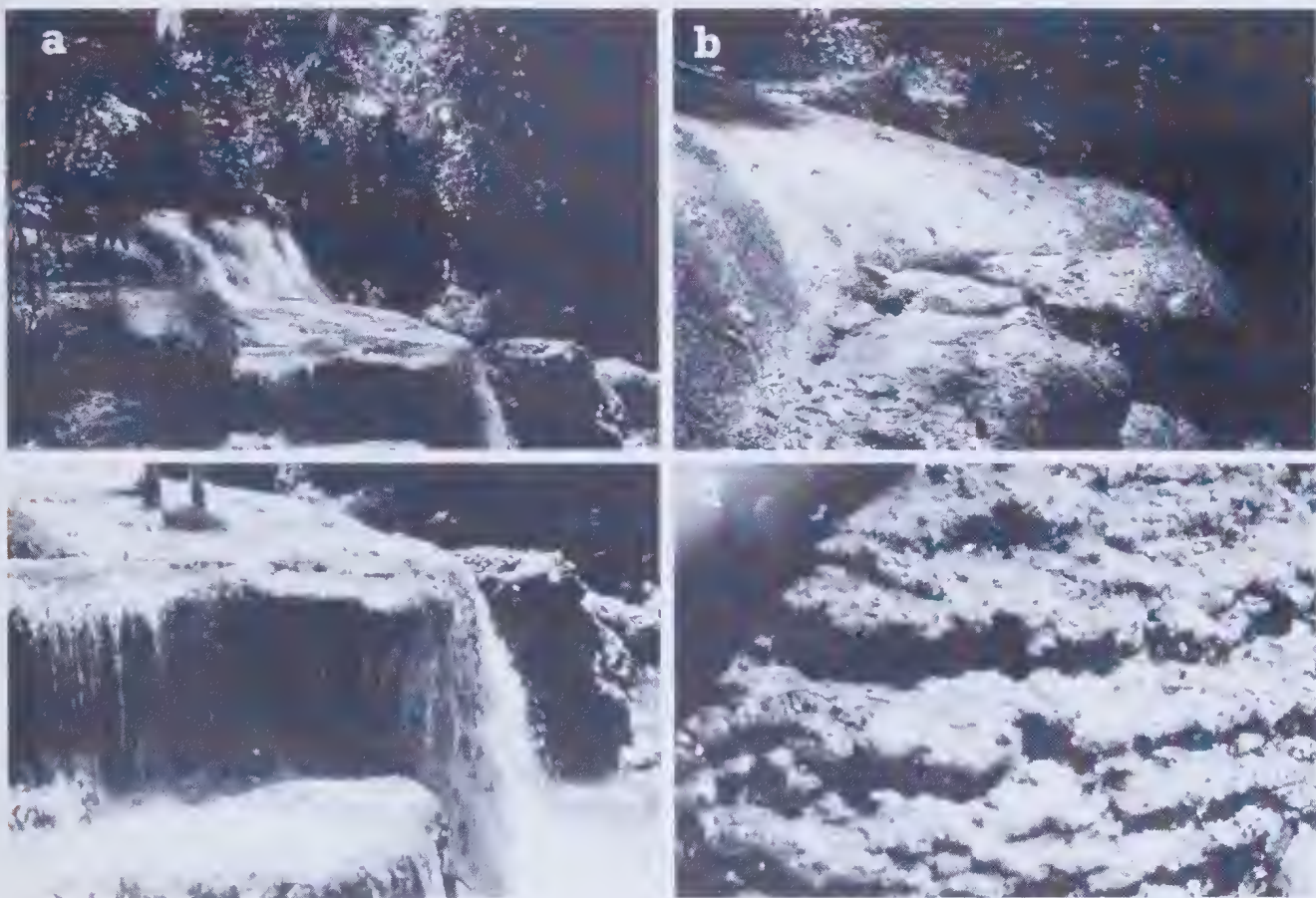


Figure 2. Parts of the Og tufa. a. general view of lower left section of Fig 3, b. 'riffle' flow over gently sloping tufa denoted by the broad tufa areas in Fig 3, c. detail of "a" showing overgrowth of lip, d. scalloped area of Fig 5 *in situ* with water partly diverted by arm (upper left).



Figure 3. Plan and extended section of the tufa deposit below Og Cave with the apparently active tufa faces shown in black. The stream emerges from Og Cave (1) and spreads through a series of pools formed by tufa dams (3-8), before the confluence with another stream below the final dam (8). Some tufa dams have a narrow sill and a nearly vertical downstream face from which the water falls (3, 5-8; see Fig 2c), while others have a broad sloping sill over which the water has a riffle flow (4, D see Fig 2b). Main dam (5); B marks the site of the sill referred to in the text; dam of the upper pool (3); D denotes sites from which tufa samples were collected; E marks the approximate site of the fracture in the lower tufa dam caused by an earthquake in 1972.

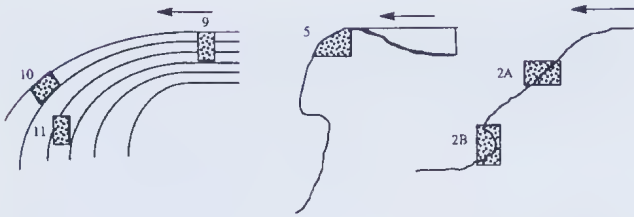


Figure 4. The location of the tufa samples: diagrammatic downstream profiles of three tufa dams indicating the relative positions from which the tufa samples were cut (numbered blocks). Left, gentle slope as in Fig 2b; middle, lip overgrowth as in Fig 2c.

sections, 151 x 176 mm in size, were prepared from six different tufa samples. These were examined under a Zeiss Photomicroscope II and Nikon SMZ stereomicroscope, with white and polarized light.

Morphological parameters of the tufa and its components (e.g. lamina thickness, size of microbes, and insect tube diameter) were analyzed using Optimas image analysis software (Bioscan). Statistics were performed using Microsoft Excel and SPSS for Windows.

Description of the tufa deposit

Overview

Owing to its proximity to Og Cave, we have named the deposit the Og tufa. The tufa is apparently unique within the extensive area known to the people of Sein (>10,000 km²) although superficial deposits of tufa, lacking dams or insect tubes, are found coating rocks associated with seepages entering the Sein River from its west bank, as well as downstream of the Og confluence. The Og tufa occurs in a gorge about 20–30 m deep and 7–40 m wide, that is fringed by lowland tropical vegetation. Hence, the solar radiation incident on the tufa deposit is quite restricted, especially close to the cave. The tufa commences within 20 m of the outflow from Og Cave and extends for approximately 60 m downstream to a confluence with another tributary. There is no visible tufa deposit at the tunnel outflow but it may be obscured by a recent rockfall. The river descends 12.5 m through a series of tufa dams over a horizontal distance of approximately 60 m (Fig 3). The volume of tufa represented in Fig 3 is estimated to be in the order of 2000 m³, assuming a constant gradient in the underlying rock. We have not measured the rate of flow for the waters in the study area.

Og Cave contains large bat colonies (thousands of bats belonging to at least several species; T Reardon, *pers. comm.* 1994), leeches (V M van der Lande, *pers. comm.* 1994), amblypygids, and millipedes. The downstream water sometimes smells of bat guano.

A fracture associated with an earthquake in 1972 split the tufa dam of the main pool near the left bank (Fig 3, site E). This caused the pool to drain and it is the only time known to the people of Sein, who use the pools daily, that water has not flowed over the face of the tufa dams. While the fissure is still visible to within 15 cm of the next drop-off, it has since been filled naturally with gravel; there has been no regrowth of tufa in the fissure. This lack of overgrowth by tufa suggests a slow rate of

tufa formation in this environment. The general morphology of the deposit and the fissure suggest that the system develops by downstream progression with only minimal vertical accretion at the rims.

The river level is reported to be have been constant, even during periods of the ENSO drought. A massive log wedged in the tunnel indicates occasional major flooding. At the time of sampling in May 1990, the mean depth of water flowing over the lip of the main dam was 19 ± 3 mm ($n=20$) and this depth was reported to be normal by the people of Sein.

The Og tufa is highly variable in morphology, especially at a fine scale, and we present our description of the tufa at four observational levels: megastructure, macrostructure, mesostructure, and microstructure (K Grey, S M Awramik, J Bertrand-Sarfati, H J. Hofmann, B R Pratt, MR Walter & Zhu Shixing, unpublished observations) and we focus on those features that stand out at the observational level under discussion.

Megastructure

The large-scale configuration of the tufa deposit, as seen in the field, consists of a series of dams, a few to several metres wide and up to 17 m long, that stand from less than a metre to four metres high above the next, lower tufa/pool complex (Fig 3). The upper pool contains a series of crescent shaped lips and their constant level and shape suggest that they represent fossil tufa dams, as found in some Australian tufa deposits (R Drysdale, *pers. comm.* 1994).

The lips occur between 8 and 22 m upstream of the retaining dam and are progressively deeper in the pooled water upstream, the successive mean depths ($\pm$ standard deviation, n) being $22 \pm 8(8)$, $32 \pm 3(8)$, and $50 \pm 1(3)$ cm.

The rims of the extant dams are up to ca. 17 m long, are level (± 3 mm), and appear to be self-regulating. A riffle-flow, several metres long, forms as the pool shallows toward the lip of the dam (the water was $19 \pm 3(8)$ mm

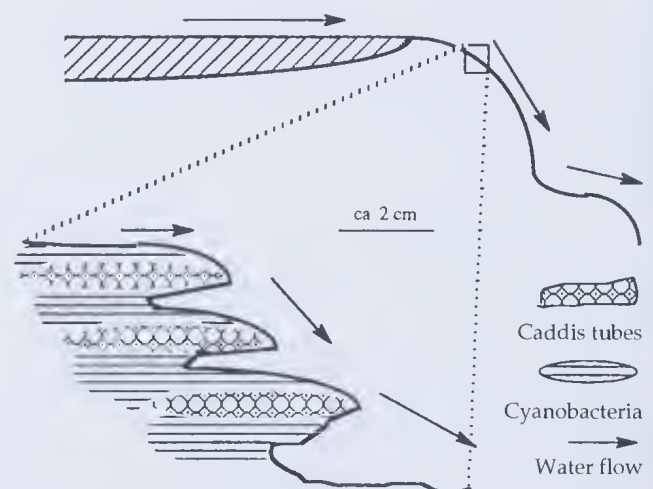
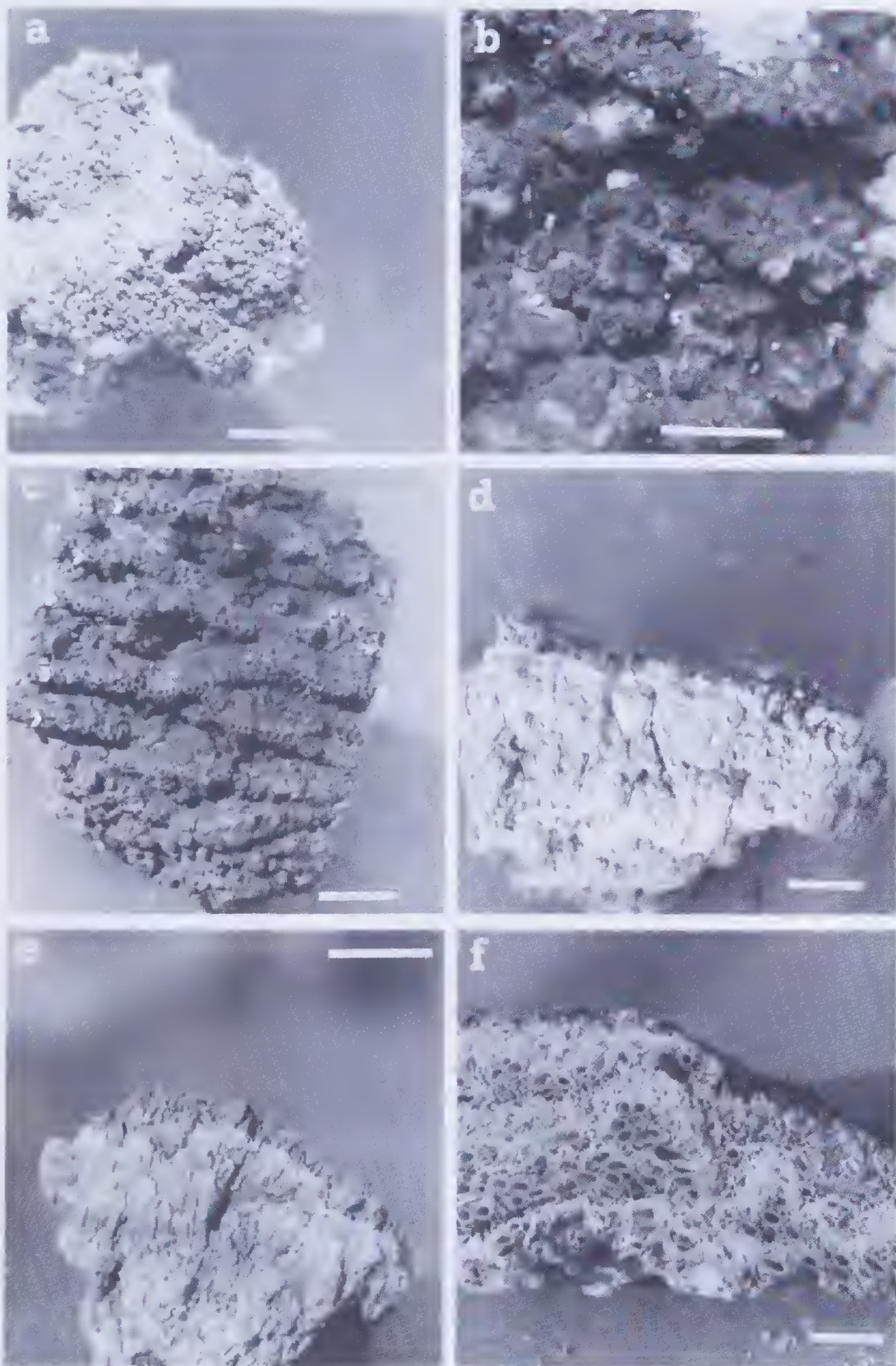


Figure 5. Diagrammatic section through an active face of the tufa formation showing water flow, and detail showing the scalloped edge (cf Fig 2d) and the location of caddis fly tubes and cyanobacteria/algal bands.



Figures 6. Photographs of the surface and gross sections of the formation at Sein. **a.** Surface of tufa upstream of the sill showing small protuberances (similar to the chou-fleur type of Freytet & Plet 1990); sample 2a in Fig 4. Scale bar = 10 mm. **b.** Surface growth forms as broad papillae on the sill; sample 2b in Fig 4. Scale bar = 10 mm. **c.** Surface view of the scalloping below the lip of the sill resulting from the alternating layers of cyanobacterial growth and insect tubes (arrows); sample 5 in Fig 4. Scale bar = 20 mm. **d.** Section of Fig 6b above showing the columnar growth form; sample 2a in Fig 4. Scale bar = 20 mm. **e.** Section of Fig 6a above showing the columnar growth form and the banding. Scale bar = 10 mm. **f.** Section of Fig 6c above showing alternating bands of calcareous insect tubes and denser 'algal' layers. Note macroalgae on the surface. Scale bar = 20 mm.

deep on the main dam at the time of sampling). Tufa is deposited on the steep downstream side of the dam and, as well as the expected 'microgours', has in some places a scalloped surface (Figs 2d, 5, 6c).

Macrostructure

The overall structure of the individual components of the tufa is termed the macrostructure. The tufa is primarily massive; nevertheless, there are certain obvious individual components of the tufa such as the banded appearance (Fig 6f) that is present even in the absence of insect tubes (Fig 6c, 6f), stromatolites (small columns, pseudocolumns, and columnar-layered structures; Fig 6d), and nodules or bumps on the surface (Figs 6a, 6b).

The surface of the tufa is dominated by bumps or nodules. These often appear as small protuberances, commonly a few millimetres in size but up to 2 cm across and up to 0.8 cm high (Figs 6a, 6b). Many of the nodules, when studied in cut specimens and in thin sections, appear to be the product of the complex growth of columnar-layered and pseudocolumnar stromatolites, some with a pillared microstructure (Figs 6a, 6e). Upstream of the sill (site B in Fig 3) the surface of the tufa is not regularly sculptured, but below the lip it is often deeply scalloped (Figs 2d, 5, 6c) with indentations on the order of 2.5 cm deep. The scalloping appears to be produced by the alignment of aquatic insect tubes (Figs 5, 6c, 6f, 7a). The general scalloping associated with the leading edge of the sill seems to be influenced by algae/cyanobacteria, an hypothesis that is supported by the highest density of stromatolites in these samples (Figs 6f, 8d).

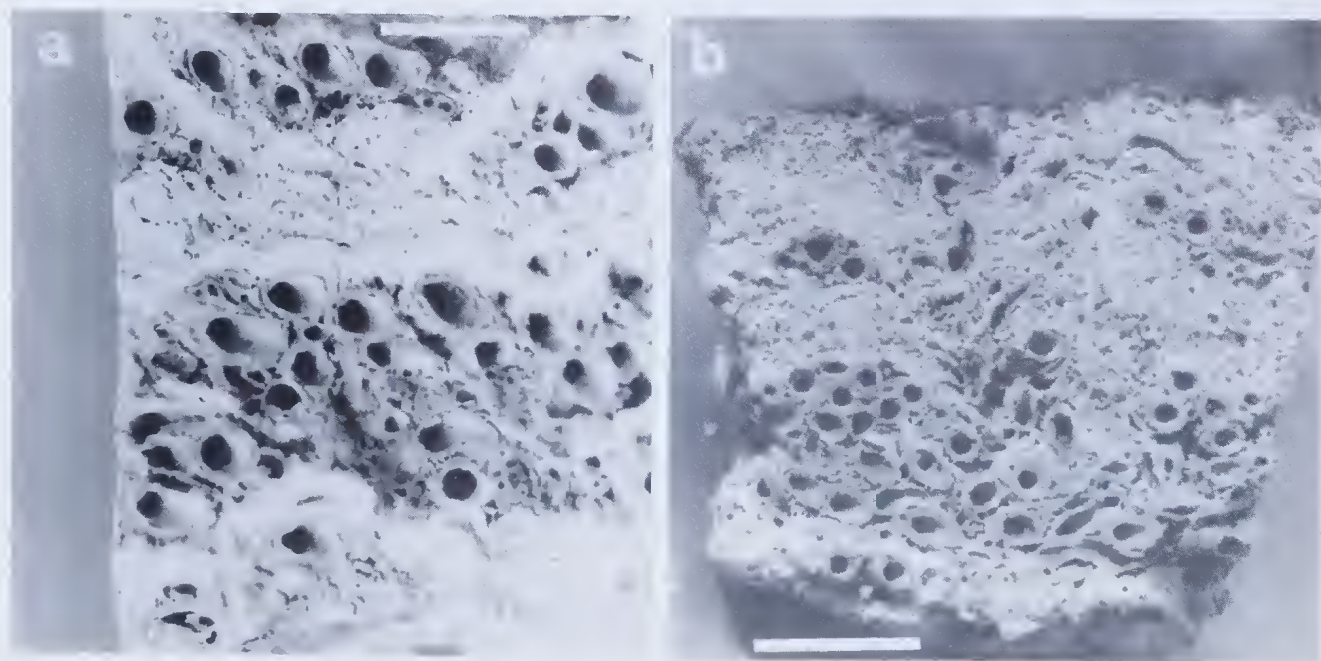
Mesostructure

The mesostructure features (at a scale between macrostructure and microstructure; see below) include

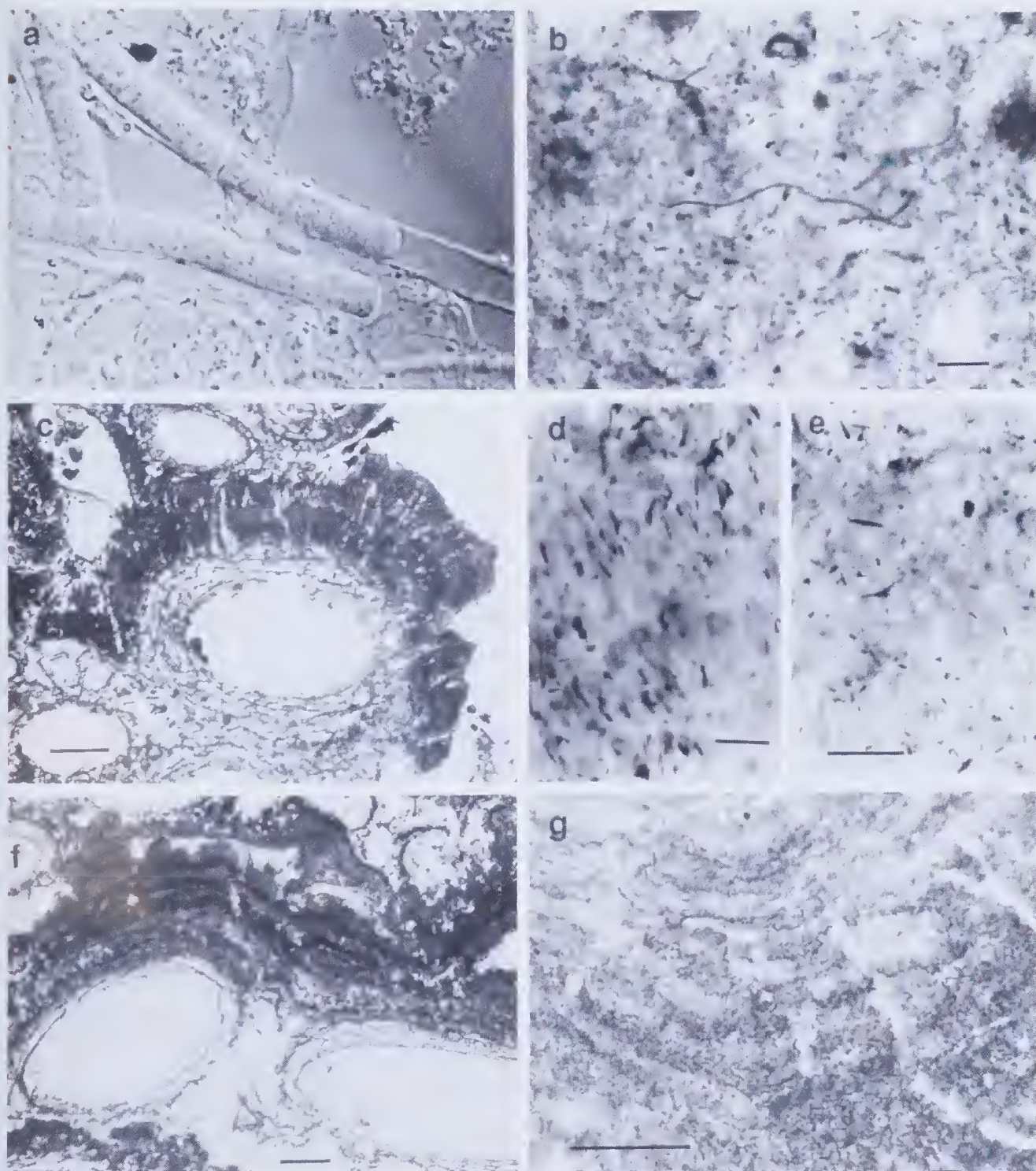
insect tubes, stromatolites and their lamination (and banding), and other small-scale features observable with the eye or hand lens.

The tufa is variable from site to site and our limited sampling constrains our ability to discern any but the most superficial patterns. Edges of dams (sills) and other areas of greater water turbulence appear to have the densest occurrence of insect tubes. Sites with denser (less porous) tufa have few large insect tubes but many smaller tubes, and a fabric that is characterized by pillared to arborescent micritic bushes often originating on insect tubes with stromatolites oriented normal to the upper surface (Fig 8c). The best-developed stromatolites (Fig 8d) occur in tufa with dense accumulations of insect tubes (Figs 6f, 8a, 8b); however, thin, somewhat columnar, columnar-layered, and pseudocolumnar stromatolites are common in all samples (terminology from K Grey, S M Awramik, J Bertrand-Sarfati, H J. Hofmann, B R Pratt, MR Walter & Zhu Shixing, unpublished observations). In samples with few insect tubes, nodules appear to be formed by pseudocolumnar tufa and stromatolite formation (Fig 6d).

The insect tubes, produced primarily by caddis fly larvae (Trichoptera), occur in all samples studied and range in size from 0.18 to 3.06 mm in diameter (mean=0.93 mm; median= 0.64 mm; n=384). They have arbitrarily been grouped into small (≤ 0.64 mm) and large (>0.64 mm) tubes. Tubes are not uniformly distributed with respect to size and density. For example, the sample illustrated in Fig 6f has dense arrays of large tubes with a mean diameter of 1.7 mm (median=1.83 mm; n=109). In another sample (SBO304) which has abundant tubes (ranging in size from 0.19 to 2.41 mm dia; mean=0.56 mm; median=0.44 mm; n=107), large tubes (>0.64 mm in diameter) are rare. Walls of the calcified tubes, which are up to 1 mm thick, are composed of



Figures 7. Gross sections of the formation at Sein. **a.** Section of Fig 6c showing alternating bands of calcareous insect tubes and denser layers which are stromatolites or microbial carbonates. Scale bar = 10 mm. **b.** End view of Fig 6f. Scale bar = 20 mm.



Figures 8. Photomicrographs of microbes in formalin preserved samples and thin sections of dried tufa. a. Oscillatorian cyanobacteria on surface of tufa (from formalin preserved sample). Scale bar *ca.* 10 μ m. b. Filamentous cyanobacteria in laminae of the stromatolites. Scale bar *ca.* 25 μ m. c. Portion of stromatolite on calcified insect tube with pillared microstructure or tufts; pillars are separated by voids filled with sparite. Scale bar = 1 mm. d. Microbial carbonate with radiating filamentous microbial fossils (clear tubes) in a micritic matrix, forming small, dense bushes. Scale bar *ca.* 25 μ m. e. Cross section of filamentous microbial fossils (arrows) similar to Fig 8d. Scale bar *ca.* 25 μ m. f. Stromatolite encrusting and bridging calcified insect tubes. Scale bar = 1 mm. g. Coarsely laminated stromatolites. Scale bar = 1 mm.

laterally discontinuous micritic layers often organized in a lacework to cellular pattern (Figs 8c, 8f). The inner surface of tubes often has a yellowish-brown stain. Tufa specimens with moderate to abundant calcified insect tubes also appear to have the most stromatolites. In thin

section, the laminae of the stromatolites are seen between and encrusting insect tubes (Fig 8f).

Frequently, a variety of small (<1 cm dia) calcareous tubes is found in tufa (e.g. Wallner 1935; Heimann & Sass 1989). Some of these are carbonate precipitated

around plants (Pedley 1992) while others are calcified insect tubes (Scholl & Taft 1964). In contemporary deposits, direct observation can be made of the organisms making the tube but in ancient tufa deposits it may be difficult to differentiate between plant and insect tubes. However, in fossilized examples a limited variability in tube diameter would suggest that small plants (e.g. bryophytes) and insects were involved, whereas tubes many centimetres in length would indicate plant stems or roots (root hairs may be preserved). We suggest that the nature of the calcified wall, like the lacework found in the Og tufa insect tubes, may be a feature characteristic of tube-building insects that could be used to identify them in ancient tufas.

The tufa contains numerous small (<1 cm dia) pseudocolumnar and columnar-layered stromatolites (columnar forms are rare), less than a centimetre high, that frequently encrust masses of calcified tubes (Fig 8f). The stromatolites appear to be most abundant in tufa with the densest population of tubes and these occur at the sill; however, they are not abundant in tufa with the fence-like arrays of tubes (Fig 6c).

The thickness of the stromatolitic laminae varies considerably. However, there is a clear pattern of predominantly light laminae (average 114.8 μm thick) and dark laminae (average 56.4 μm thick). Some areas have a coarsely laminated, banded appearance (Fig 8g) which is a variety of stromatolitic laminae (Fig 8f). The bands are alternating layers of thinner dark micrite and thicker light-colored microspar and differ from stromatolite laminae in their more diffuse boundaries and overall coarseness of the calcite. Unlike banding in many lacustrine stromatolites, these bands are not composed of finer laminations.

Microstructure

Much of the tufa is structureless and composed of micrite with numerous voids. Thin sections of this tufa appear very dull, blue-green in color under cathode luminescence indicating primary, fresh calcite that has not been influenced by meteoric/diagenetic processes. There are two obvious microstructures, pillared and stromatolitic. Stromatolitic microstructure consists of alternating laminae of thinner dark micrite and thicker light microsparite (see above). The preservation of the material is sufficient to preserve filamentous microbial fossils (presumably cyanobacteria) in the laminae (Fig 8b).

An interesting microstructure is a pillared form which is dominant in sample SBO 305. The pillars consist of small, possibly cylindrical structures (25 to 82 μm dia), some occasionally bifurcate, arranged in a radial manner on large calcified insect tubes, and composed of micrite (Fig 8c). Individual pillars have a fibrous internal structure and are composed of remnants of microbial filaments arranged parallel to the long axis of the pillar. This structure resembles the stromatolitic tufts described by Freytet & Plaziat (1982, Plate 9a on page 113). Most filaments are not well preserved and it is uncertain if the filaments branch. The diameter of filament moulds of clear calcite is approximately 3 μm . Filaments of this size are apparently common in tufa (e.g. Pedley 1987).

Biogenic elements in the tufa

Cyanobacteria and algae. In formalin preserved specimens, the surface of the tufa contains a complex microbial community dominated by filamentous cyanobacteria (Fig 8a) and diatoms. Green algae live on the surface of the tufa, but we have not found compelling evidence of green algae preserved in the tufa. The pillared microstructure shown in Fig 8c contains in longitudinal section what might appear to be the remains of large filaments. However, we have not found circular cross sections of the same diameter that would support this interpretation (see Figs 8d, 8e). While the cyanobacteria appear to dominate numerically, the larger green algae would dominate the photosynthetic biomass. Because of limited sampling of fixed material and the degradation that occurred between the time samples were collected and fixed in the laboratory, we have not attempted to identify the cyanobacteria or algae in more detail.

Fauna. An abundant and diverse fauna is sometimes found in and on tufa deposits (e.g. Dürrenfeldt 1978) and the Og tufa is no exception. Faunal samples were taken for identification from a number of distinct habitats within the system. The dominant biomass of these samples is for several species of sedentary caddis fly (Trichoptera), Diptera ('midges') and aquatic lepidopteran larvae (Pyrilidae; two species). Some of these species inhabit tubes in the tufa, and spin nets.

Adult Trichoptera collected represent eight genera (ca. 14 species; Table 1). Larvae were present in various instars at the one time observed. Adults of the dipteran family Chironomidae represent probably eight species of eight genera (P Cranston, *pers. comm.*). The lepidopteran family Pyralidae was represented by larvae of probably one genus (Table 1; the subfamily Nymphulinae within Australasia requires revision; J Hawking, *pers. comm.*). In addition, an errant fauna including flatworms (Turbellaria) and water mites (Hydracharina) was observed.

Many of the caddis-fly larvae (Trichoptera: Hydropsychidae: Philopotamidae) represented in the samples mostly strain food (algae, fine organic particles and small invertebrates) from the flowing water by constructing capture nets of silk. Leptoceridae may be large or small particle detritivores with some tendency to herbivory (especially in *Trienodes* PT-773), or predatory (St Clair 1994). Larvae of the predatory Leptoceridae construct tubular cases of mineral and plant materials, and the Hydroptilidae, or micro-caddises, are free-living for the first four instars and only construct a purse-shaped case in the fifth instar (Neboiss 1991).

The Nymphulinae (Lepidoptera) have aquatic larvae which may be case-making, web-spinning or free-living, and feed on algae or aquatic plants, and may live in flat cases formed from pieces of the food plant.

The chironomid taxa represented are all rheophilic, with the possible exception of ?*Bryophaenocladus*, which belongs to a terrestrial/semi-terrestrial clade. Most are relatively cosmopolitan genera, although *Riethia* has South American/Australian affinities, and *Skusella* has Afrotropical/Australian affinities. *Microtendipes* is apparently monotypic and quite uncommon in Australia, and the only adult species that has been named is

Table 1

Insect larvae (L) identified from the tufa, and adults (A) collected at a black light situated above the Og tufa.

Species	Family
TRICHOPTERA	
<i>Cheumatopsyche</i> sp PT-1862	Hydropsychidae (A)
<i>Cheumatopsyche</i> sp PT-1863	Hydropsychidae (A)
<i>Cheumatopsyche</i> sp PT-1868	Hydropsychidae (A)
<i>Cheumatopsyche</i> sp	Hydropsychidae (L)
<i>Chimarra</i> sp PT-1864	Philopotamidae (A)
<i>Chimarra</i> sp nr <i>C. goroka</i> Sykora PT-1866	Philopotamidae (A)
<i>Chimarra</i> sp nr <i>C. papuana</i> Kimm. PT-1865	Philopotamidae (A)
<i>Chimarra</i> sp	Philopotamidae (L)
<i>Ecnomus</i> sp	Ecnomidae (A)
<i>Hellyethira</i> sp nov A Wells (in press)	Hydroptilidae (A)
<i>Oecetis</i> sp; ? <i>O. buitenzorgensis</i> Ulmer	Leptoceridae (A)
<i>Orthotrichia</i> sp nov ¹	Hydroptilidae (A)
<i>Tinodes</i> sp; ? <i>T. aberrans</i> Kimm	Psychomyiidae (A)
<i>Triaenodes</i> sp PT-1867	Leptoceridae (A)
<i>Triaenodes</i> sp B	Leptoceridae (A)
?genus	Leptoceridae (L)
<i>Triaenodes</i> sp C (different from PT-1867)	Leptoceridae (A)
?genus sp 2	Hydrophilidae (L)
DIPTERA: CHIRONOMIDAE	
genus nr <i>Thienemannimyia</i>	Tanypodinae: Pentaneurini
<i>Cricotopus</i> cf <i>albitibia</i> Kieffer	Orthocladiinae (A)
<i>Riethia</i> ?stictoptera	Chironominae (A)
<i>Rheotanytarsus</i>	Chironominae (A)
<i>Rheocricotopus</i>	Orthocladiinae (A)
nr <i>Bryophaenocladus</i>	Orthocladiinae (A)
genus nr <i>Skusella</i>	Chironominae (A)
<i>Microtendipes</i> sp	Chironominae (A)
LEPIDOPTERA: PYRALIDAE	
<i>Potamomusa</i> sp	Nymphulinae (L)
EPHEMEROPTERA	
?genus	Caenidae (L)
<i>Baetis</i> sp	Baetinae (L)

¹ to be described by A Neboiss

conspecific with the Afrotropical species, although rearing would be required to confirm this (P Cranston, pers. comm.).

Water chemistry

The general water chemistry from samples collected above and below the Og tufa are presented in Table 2. The pH of the water increased significantly while flowing over the formation rising from pH 7.6 to ca. pH 8.0 ($F_{1,4} = 36.7$; $p = 0.004$) but the temperature ($26.7 \pm 0.33^\circ\text{C}$; $n=10$) and oxygen content (mean 7.8 ± 0.13 ppm O_2 , $n=14$) showed no trend, with the latter being ca. 95-99% saturated throughout its passage across the formation. The water is nutrient rich (as reflected by the nitrate levels; Table 2) having received the waste products of a large bat colony inhabiting the tunnel immediately upstream.

Table 2

The mean constituents of water flowing over the Og tufa on 24 May 1990 ($n=2$).

	mg L ⁻¹
Calcium	27.65
Magnesium	2.15
Potassium	0.35
Sodium	2.3
Total iron	0.34
Nitrite-N	0.006
Nitrate-N	0.47
Ammonium-N	0.39
Phosphate-P	0.025
Total-P	0.031

The water chemistry is unremarkable except that the calcium concentration of <30 mg L⁻¹ is very low for a tufa-depositing stream and perhaps provides support for the biotic involvement in the tufa formation. By comparison, fresh groundwater in a tropical karst in Cape Range, Western Australia, has a mean of 82 mg L⁻¹ Ca²⁺ ($sd = 4.9$, $n = 7$). Detailed examination of the water and tufa chemistries is required to determine the relative contribution of physical and biological processes to tufa deposition and nature of the carbonates involved.

Microenvironment

The water velocity increases as it approaches the lip of the sill (dam) and passes down the face. The distribution of the taxa with respect to the sills in the tufa is shown in Fig 9. The front face is saw-toothed with the lee positions of the formation being occupied by tubes of net-making caddis flies; the growth appears to be by forward progression of the cyanobacteria-rich laminae (Fig 5). The internal structure of the formation varies in a manner apparently related to the nature of the water flow in the area. Sections of the rock show clearly that tufa growth has progressed outwards and that it has changed position (elevation; see fossil sills in Fig 3) so that the deposited band of tufa/calcite is sinuous, similar to turbulent water flow (Figs 6f, 7a, 7b).

The rows of net-trapping Trichoptera were mostly collected under the overhangs on the face of the dams, while the bigger, long-jawed caddis flies were more frequent in the riffles, with tube-living chironomids throughout. These are different microhabitats even within the front face of the falls. The microturbulence of the water may be of considerable importance in determining suitable microhabitats for the cyanobacteria, algae, and the arthropods.

Although many of the insects inhabiting the formation are net-builders, they would trap little non-calcareous material from the stream; the acid insoluble fraction of the tufa comprised only 0.8% by weight (range 0.30 to 1.0; $n=3$); this compares with from 4-9.1% acid insoluble fraction in tufas from Europe and Australia (Viles & Goudie 1990) and a mean of 3.44% (range 1.0-10.55%) in ten accreting deposits from active sites in Great Britain (Pentecost 1993).

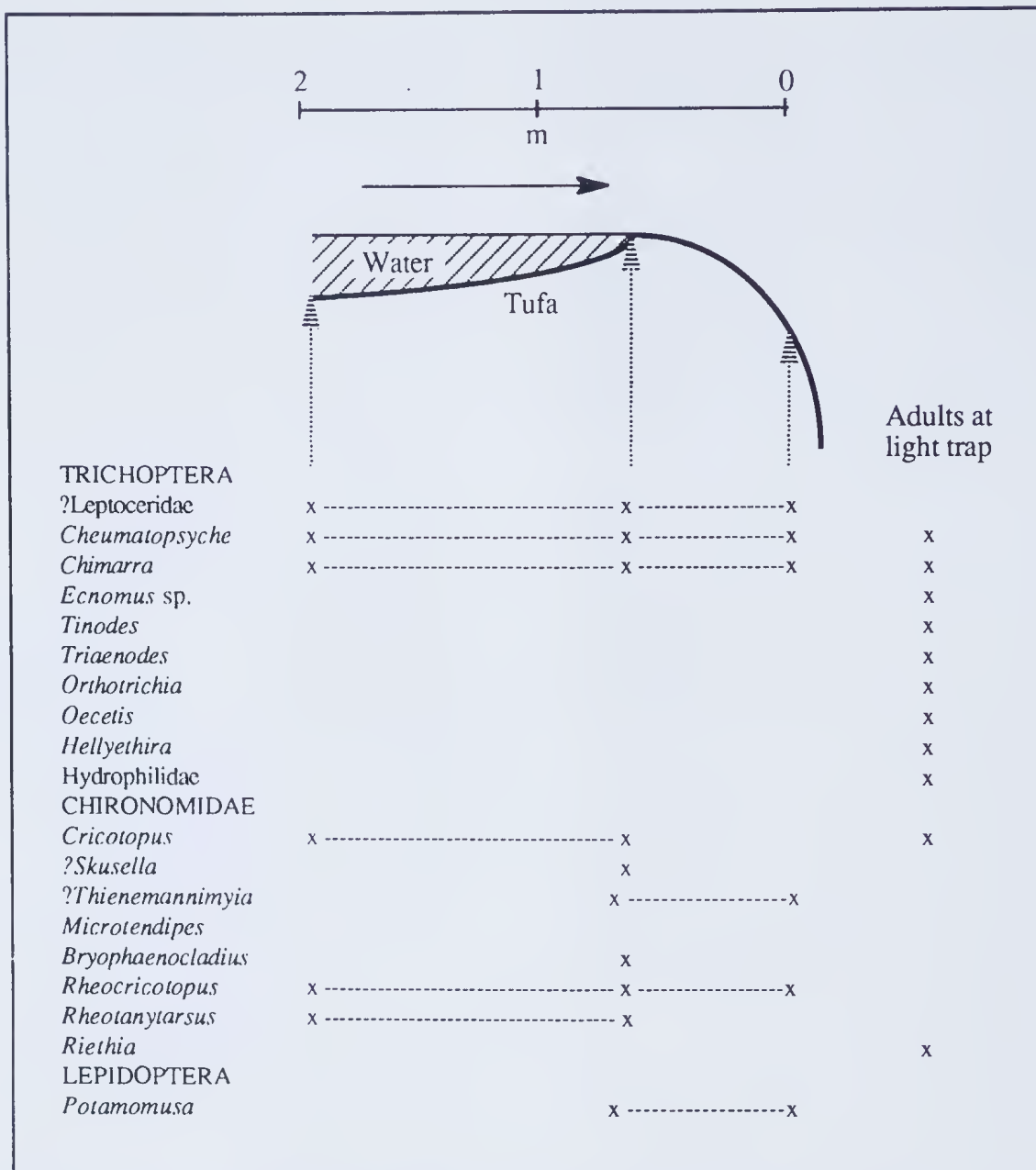


Figure 9. The distribution of the taxa with respect to the sills in the tufa formation. The water is pooled upstream of the sill and then forms riffles over the lip and down the face. The light trap data indicate adults present at the site.

Discussion

The series of drowned tufa dams in the upper pool (Fig 3; another example is also discussed by Ford 1989) provides evidence consistent with the face of the tufa dams both growing in height and progressing downstream. The sweeping convex downstream faces and the remarkable evenness of the lips of the tufa dams suggest they are self-regulating and that they progress most rapidly where the current is strongest in the centre of the stream.

The water is rich in nitrates (Table 2) possibly resulting from bat guano. Marine stromatolites are often prevented from forming by an increase in the nutrient levels in the water which promotes growth of algae over the cyanobacteria (Pentecost 1978, 1992) and the same could occur in non-marine environments. However,

with the Og Tufa, algae (other than diatoms) and mosses are not sufficiently abundant, despite the high nutrient levels, to dominate tufa surfaces and prevent cyanobacterial and diatom participation in the construction of the tufa. It is uncertain what factor(s) prevents luxurious growth of higher photosynthesizers.

Tufa dams and terraces are normally discussed in the context of examples from highly seasonal climates in which both diurnal and annual growth layers can be observed in the formations (Ford 1989). Ford's recent review mentions no large tufa deposits from equatorial regions lacking seasonality – the constancy of water flow over the Og tufa was noted above – yet widespread and varied tufa deposits were reported by Hossfeld (1951) to occur in northern Papua New Guinea, including the Madang area.

Five methods of tufa deposition have been identified (Ford 1989): 1) chemical reactions in saline or alkaline lakes; 2) the cooling of thermal waters 3) inorganic degassing of CO₂ (often promoted by microturbulence); 4) indirect biochemical precipitation caused by photosynthetic uptake of CO₂; and 5) direct metabolic precipitation of calcium carbonate by organisms such as cyanobacteria, algae, and mosses. The first two factors are unlikely candidates for the genesis of the Og tufa because the conditions are not appropriate. The third factor is unlikely to be the prime agent in the formation of the Og tufa as there is only minor evidence for tufa formation where it might be expected elsewhere in the system, in the absence of biotic associates. The fourth factor is unlikely as living stems and leaves immersed in the water were not covered by tufa either above or below the Og tufa. The presence of cyanobacteria and algae within the tufa and the development of stromatolites within suggest a role of the fifth factor in the formation of the Og tufa, although the effect might be indirect (Pentecost 1978, 1981, 1984, 1985).

Our study of the Og tufa suggests that a sixth factor needs to be added to the list of tufa depositing agents, namely the presence of tube-building insects living amongst the stromatolitic layers (Figs 6f, 7a, 7b, 8a, 8b). The tubes provide a stable substrate for benthic microbes (like the cyanobacteria and diatoms) that are adapted to an environment characterized by turbulence and the precipitation of calcium carbonate.

The Og tufa is an example of a tufa deposit formed by a combination of factors (3, 5, and 6) where local water turbulence, a rich benthic photosynthetic microbial community, and calcite tube-building invertebrates combine to form tufa.

There is a commonly held notion that microbial mats and stromatolites form in environments that are extreme (e.g. Jørgensen & Revsbech 1982). Microbial mats of cyanobacteria and diatoms are very common in a variety of environments and form in areas actively grazed and burrowed by macro and micro invertebrates. The accretion of cyanobacteria into stromatolites in an environment seemingly benign - constant water, equatorial climate, buffered, moderate water chemistry - and biotically rich may be puzzling. However, the key ingredient here is the rapid precipitation of calcite that mineralizes the structure; if mineralization is contemporaneous with microbial growth, stromatolites can form.

Acknowledgements: We are grateful to the landowners of Sein village for permission to work in the area, for their assistance with the work and their hospitality. For determining the fauna we thank Dr A Neboiss, Museum of Victoria (Trichoptera); Mr J Hawking, Murray Darling Fresh Water Research Centre, Albury (Pyralidae) and Dr P Cranston, Australian National Insect Collection (Chironomidae). Laboratory water analyses were conducted by P L Osborne, Department of Biology, University of Papua New Guinea. Caroline Lawrence assisted in the preparation of the map and Douglas Elford printed photographs of the tufa samples. David Pierce performed the XRD analysis and printed photomicrographs. SMA acknowledges the financial assistance of NASA Grant NAGW-1940 on lacustrine stromatolites. The field work was conducted while WFH was in receipt of a Christensen Research Institute Fellowship and with the approval of the Madang Provincial Council. This is contribution 143 from the Christensen Research Institute, Madang, Papua New Guinea. We thank Russell Drysdale for his pertinent comments on a draft of this paper.

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Recent Advances in Science in Western Australia

Earth Sciences

Palaeomagnetic dating of dolerite dykes and sills in the Mesoproterozoic Albany Mobile Belt and Neoproterozoic Stirling Range Formation by researchers from the University of Western Australia provides evidence for extensional events between Australia, east Antarctica and Greater India. Three periods of dyke and sill intrusion are distinguished. The first, earliest Cambrian, phase took place during crustal extension between the Yilgarn and east Antarctic cratons and is related to Gondwana assembly. A second phase of mid-Carboniferous dykes and a third, possibly Triassic, phase are related to rifting and extension between Greater India and the Western Australian Shield during early stages in the formation of the Perth Basin.

Harris LB & Li Z X 1995 Palaeomagnetic dating and tectonic significance of dolerite intrusions in the Albany Mobile Belt, Western Australia. *Earth and Planetary Science Letters* 131:143-164.

Lithographic strata of the traditional "laterite profile" (*i.e.* pallid zone, mottled zone, laterite, 'residual' sand) and late Cenozoic valley fills of the "palaeodrainage system" (*i.e.* hardpan, calcrete, alluvium, colluvium) throughout the Yilgarn Sandland Region have been re-interpreted to be mainly desert-aeolian sediment. The traditional approaches used to resolve the origin of these units (*e.g.* photogeology, geomorphology, pedology, geochemistry) are concluded by the authors to be largely inappropriate and to have resulted in models that incorrectly interpret "laterite profile" units solely as deeply weathered basement rocks. If the regolith is to be correctly interpreted, then the authors suggest that the traditional residual and "locally reworked" views, and the alternative aeolian views, need to be investigated and critically appraised from the perspective of sedimentary geology.

Glassford D K & Semeniuk V 1995 Desert-aeolian origin of late Cenozoic regolith in arid and semi-arid Southwestern Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 114:131-166.

Intracratonic sedimentation started in the onshore northern Perth Basin in the Early Permian and continued until the breakup of Gondwana in the early Cretaceous. While mature source rocks are widespread, reservoirs are abundant, and structures are well timed for hydrocarbon entrapment, a critical factor is seal since structures covered by shales that are thinner than the throw of faults may lose their trapping potential. The Allanooka High, Dongara Terrace, Beharra Springs Terrace and Cadda Terrace — with good source rock potential, Early Triassic seals and Late Permian objectives at drillable depths — are thought to offer the best chances for further hydrocarbon discoveries.

Crostella A 1995 An evaluation of the hydrocarbon potential of the onshore Perth Basin, Western Australia. Geological Survey of Western Australia. Report 43.

Potentially economic coal seams in the Permian Irwin River Coal Measures (IRCM) on the Irwin Terrace are described by researchers from the Geological Survey of WA to cover an area of about 170 km². The IRCM and underlying sedimentary rocks constitute a broadly

upward-coarsening glaciomarine alluvial deltaic succession. Most of the coal resources are deep, with possibly 5% lying in the current opencut window. The estimated coal resources are 1000 Mt inferred (Class 1) of the Australian Code. In general, the coal is high in moisture (20-30%), high in volatiles (24-37%), moderate to low in sulphur (0.5%) and moderate to high in ash (7-30%); specific energy is between 16.38 and 21.66 MJ kg⁻¹ on an as-received basis.

Le Blanc Smith G & Mory A J 1995 Geology and Permian coal resources of the Irwin Terrace, Perth Basin, Western Australia. Geological Survey of Western Australia. Report 44.

Groundwater in the Mesozoic and Cenozoic succession is currently exploited to provide about 40% of scheme water to the Perth region; the remainder comes from surface water catchments. Perth will become more dependent on groundwater as urban development continues to expand and the surface catchments become fully utilized. Under present landuse conditions, the maximum projected total and sustainable groundwater from the aquifers in the region would be about 500 10⁶ m³ year⁻¹, and may be raised to 600 10⁶ m³ year⁻¹ with further urban development and increased groundwater recharge from stormwater catchments. The current abstraction rate of about 300 10⁶ m³ year⁻¹ is well within sustainable limits and potential exists for significant additional abstraction.

Davidson W A 1995 Hydrogeology and groundwater resources of the Perth region, Western Australia. Geological Survey of Western Australia. Bulletin 142.

The stromatolite forms *Acaciella australica* and *Basisphaera irregularis* are recorded from the Skates Hill Formation by K Grey of the Geological Survey of WA. These forms support correlation of the unit with the Bitter Springs Formation and other units of Supersequence 1 in the Centralian Superbasin, and indicate a Neoproterozoic age for the Savory Basin succession.

Grey K 1995 Neoproterozoic stromatolites from the Skates Hills Formation, Savory basin, Western Australia, and a review of the distribution of *Acaciella australica*. *Australian Journal of Earth Sciences* 42:123-132.

Life Sciences

The survival of adult western long-billed corellas and Major Mitchell cockatoos, studied in the wheatbelt of Western Australia from 1977 to 1983 by researchers from the CSIRO Division of Wildlife and Ecology (Midland), ranged from 81.3% for female Major Mitchell cockatoos (92.9% for males) to 94.2% for male western long-billed corellas (93.2% for females). The survival of immature birds was lower. This is attributed to predation of immature birds in locally nomadic flocks; immature survival was only slightly negatively affected by dispersal. The populations of both western long-billed corellas and Major Mitchell cockatoos are predicted to be stable, or slowly increasing, as appears to be the case.

Smith G T & Rowley I C R 1995 Survival of adult and nestling western long-billed corellas, *Cacatua pastinator*, and Major Mitchell cockatoos, *C. leadbeateri*, in the wheatbelt of Western Australia. *Wildlife Research* 22:155-162.

A collaborative study by researchers from the Swedish University of Agricultural Sciences and Curtin University of Technology documented the invasion of native sclerophyll woodland vegetation by exotic weed species, after fire, in linear remnants along a highway in south-western Australia. The most common weeds were the perennial grasses *Eragrostis curvula* and *Ehrharta calycina*. The weeds spread mainly from the road side of the linear sclerophyll remnants, rather than the fence side. Grasses are normally an insignificant component of sclerophyll forest, and their presence after fire increases the fire proneness. The impact of fire was still evident after 7 years. Restrictions on the frequency of burning, and on further narrowing of the linear sclerophyll woodland corridors are advocated.

Milberg P & Lamont B B 1995 Fire enhances weed invasion of roadside vegetation in southwestern Australia. *Biological Conservation* 73:45-49.

The relationship between species and genus richness of local Australian ant faunas is examined by A Andersen, of the CSIRO Tropical Ecosystems Research Centre (Winnellie), to test the validity of the hypothesis that higher-taxon categories be used, rather than species, in rapid biodiversity surveys. Although the relationship between species and genus richness was strong within regions for 24 sites distributed throughout Australia, overall it varied substantially and there was only a weak relationship. The relationship was confounded by biogeographic factors and influenced by sampling area and intensity. It is concluded that genus richness of ants is an unreliable substitute for species richness except in limited circumstances, and it is suggested that this conclusion may also apply to other taxa for which a small number of genera can contribute a large number of species.

Andersen A N 1995 Measuring more of biodiversity: genus richness as a surrogate for species richness in Australian ant faunas. *Biological Conservation* 73:39-43.

Estimates by researchers from the Department of Conservation and Land Management, Perth, of the susceptibility to *Phytophthora cinnamomi* of plant species in 63 active disease centres and 17 old centres of *Eucalyptus marginata* forest, north of the Preston River, indicated that the impact was intermediate (scattered deaths) in 46% of the active disease centres and high (most susceptible plants dead) in 29% of active centres, compared to a high impact in 65% in old disease centres. Cross tabulation of species by frequency of death and isolation of

P. cinnamomi from plant and soil allowed the classification of the response of plant species to infection.

Shearer B L & Dillon M 1995 Susceptibility of plant species in *Eucalyptus marginata* forest to infection by *Phytophthora cinnamomi*. *Australian Journal of Botany* 43:113-134.

Researchers from the Department of Conservation and Land Management, Perth, have extended the geographic and host range of the canker fungus *Cryptodiaporthe melanocraspeda*. Large numbers of *Banksia coccinea* were observed dying downward from apical branches, in the south coast region of Western Australia, in 1989; rapid complete death of stands was typical for many diseased stands. Lesions of *C. melanocraspeda* girdled stems and were concluded to be associated with the death of *B. coccinea*. In contrast, the fungi *Zythiostroma* spp, which form lesions that girdle the stems of *B. coccinea*, and *Botryosphaeria ribis*, which forms non-girdling lesions, were considered to be only weak pathogens.

Shearer B L, Fariman R G & Bathgate J A 1995 *Cryptodiaporthe melanocraspeda* canker as a threat to *Banksia coccinea* on the South Coast of Western Australia. *Plant Diseases* 79:637-641.

Note from the Hon Editor: This column helps to link the various disciplines and inform others of the broad spectrum of achievements of WA scientists (or others writing about WA). Contributions to "Recent Advances in Science in Western Australia" are welcome, and may include papers that have caught your attention or that you believe may interest other scientists in Western Australia and abroad. They are usually papers in refereed journals, or books, chapters and reviews. Abstracts from conference proceedings will not be accepted. Please submit either a reprint of the paper, or a short (2-3 sentences) summary of a recent paper together with a copy of the authors' names and addresses, to the Hon Editor or a member of the Publications Committee: Dr S D Hopper (Life Sciences), Dr A E Cockbain (Earth Sciences), and Assoc Prof G Hefter (Physical Sciences). Final choice of articles is at the discretion of the Hon Editor.

"Letters to the Editor" concerning scientific issues of relevance to this journal are also published, at the discretion of the Hon Editor. Please submit a word processing disk with letters, and suggest potential reviewers or respondents to your letter.

P C Withers, *Honorary Editor, Journal of the Royal Society of Western Australia.*

An early Triassic fossil flora from Culvida Soak, Canning Basin, Western Australia

G J Retallack

Department of Geological Sciences, University of Oregon, Eugene, Oregon USA 97403

Manuscript received May 1995; accepted October 1995

Abstract

New collections of fossil plants and reinterpretation of previous paleobotanical work indicate that the Culvida Sandstone is late Early to early Middle Triassic (late Scythian-Anisian), or some 244-248 Ma in age. Most of the fossils have been identified with well known species, with the exception of *Chiropteris whitei* sp nov and *Pleuromeia dubia* (Seward) comb nov. This fossil flora is most similar to that of the Newport and Camden Haven Formations of New South Wales. There are also strong similarities with the fossil flora of the Parsora Beds of the South Rewa Basin, India, and the Burgersdorp Formation of South Africa. The Culvida flora is dominated by *Dicroidium zuberi* like southeastern Australian floras of humid cool temperate paleolatitudes, but it also contains *D. hughesii* which dominated monsoonal subtropical floras of India and South Africa. The Culvida flora was thus transitional between these two floristic regions. Despite these regional differences in dominance, early Triassic floras were surprisingly cosmopolitan and low in diversity following the Permian-Triassic life crisis.

Introduction

The early Triassic was peculiar for world vegetation because of low diversity cosmopolitan floras (Retallack 1995). The homogeneity of early Triassic floras across the great Pangean landmass presents a challenge to modern concepts of uniformitarianism, and is in stark contrast to diverse and provincialized floras of the late Permian and Middle Triassic. Low diversity early Triassic fossil floras have been found in Argentina, New South Wales, central Queensland and Tasmania, all high latitude humid parts of the Gondwana supercontinent (Retallack 1977). The Canning Basin of Western Australia is one of the few regions with Early Triassic fossil floras from the low latitude northern edge of the supercontinent. This paper describes one of these fossil floras that have remained until now poorly known.

A newly described collection

A collection of fossil plants was made in 1973 by G R Evans and L N Brown of Mines Administration Pty Ltd of Brisbane, and forwarded to me for study by R J Paten. The specimens are now housed under numbers F9143 to 9160 in collections of the Geological Survey of Western Australia.

The fossils are impressions in white shale, with irregular areas of red and purple stain. This colour is typical for the mottled zone of a deep lateritic paleosol, and is presumed to be a Cenozoic alteration of a pre-existing Triassic plant-bearing shale that may have been grey to brown in color. The fossils were collected from the Culvida Sandstone at Culvida Soak (Fig 1: grid reference 506468 on Cornish 1:250,000 sheet). The matrix of the fossils is most similar to the interval 140-170 m

above the base of the Culvida Sandstone in BMR Cornish number 2 borehole (Yeates *et al.* 1975).

The following fossil species were identified from this collection and are discussed in more detail at the end of this paper.

Pleuromeia dubia (Seward) comb nov
Cladophlebis carnei Holmes & Ash 1979
Chiropteris whitei sp nov
Dicroidium hughesi (Feistmantel) Lele 1962a
Dicroidium narrabeenense Jacob & Jacob 1950
Dicroidium zuberi (Szajnoch) Archangelsky 1968
Umkomasia sp indet
Lepidopteris madagascariensis Carpentier 1935

Reinterpretation of previous collections

Earlier paleobotanical work by White (1961) and White & Yeates (1976) can now be revised. Updated lists for localities (Fig 1) currently recognized within the Culvida Sandstone (by Yeates *et al.* 1975) are given below, with commentary following.

- CO8 Equisetales gen et sp indet (White 1961 Pl 2, Figs 5,6, Pl 3, Fig 1)
 Dicroidium zuberi (Szajnoch) Archangelsky 1968 (White 1961)
 Taeniopteris sp indet (White 1961)
- CO62 *Dicroidium hughesii* (Feistmantel) Lele 1962a (White 1961, Pl 3, Fig 6)
 Dicroidium narrabeenense (Walkom) Jacob & Jacob 1950 (White 1961, Pl 3, Figs 3,4B)
 Pteruchus barrealensis (Frenguelli) Holmes & Ash 1979 (White 1961, Pl 3, Fig 4A)
 Chiropteris whitei sp nov (White 1961, Pl 3, Fig 5)

Thus, the Culvida Sandstone is about the same age as the Erskine Sandstone and Blina Shale, which successively underlie the Culvida Sandstone in the Canning Basin. The Blina Shale has also yielded the lycopsid *Pleuromeia indica* (Lele) Dobruskina (1985: see White & Yeates 1976, Pl 6, Figs 18-21, Pl 12, Figs 42-44) as well as a sparse marine fauna (Gorter 1978). Plant fossils from the Erskine Sandstone include the characteristic rounded sporophylls, as well as other remains of *Pleuromeia sternbergi* (Münster) Corda in Germar (1852: see Foord 1890; Brunnschweiler 1954; White & Yeates, 1976, Pl 6, Fig 17b, Pl 8, Fig 29) as well as abundant *Dicroidium zuberi* (Szajnoch) Archangelsky (1968: see Antevs 1913; Townrow 1957). These rock units probably represent beach ridges and coastal lagoons respectively, outboard of the fluvial Culvida Sandstone. Marine regression that created the general sequence Blina-Erskine-Culvida Formations in the Canning Basin (Gorter, 1978) also created the correlative sequence of Garie-Newport Formations in the Sydney Basin (Retallack 1975, 1980a).

Paleoecology and paleoclimatology of Culvida Soak

The Culvida Soak fossil flora has most plants of the *Dicroidietum zuberi* fossil plant association of eastern Australia (Retallack 1977). This was a broadleaf flora dominated by the extinct seed fern *Dicroidium zuberi*, whose presence is confirmed for the Culvida flora by its characteristic pollen-bearing and ovuliferous organs. This widespread early Triassic assemblage was probably a heath or forest assemblage of nutrient poor soils. These indications of oligotrophy include low species diversity and thick leathery leaves. The Culvida Soak flora shows rather smaller leaf size in *Dicroidium zuberi* and *D. narrabeenensis*, and fewer pteridophytes than comparable floras of eastern Australia, and this may be an indication of a drier climate.

The Culvida flora also contains a few specimens of *Dicroidium hughesii*, which is the dominant taxon of a fossil plant association that can be termed the *Dicroidietum hughesii*. Based on the fossil flora of the Burgersdorp Formation near Aliwal North, South Africa, this association contains a variety of pinnate cycadophyte and ginkgolike leaves not found in early Triassic floras of southeastern Australia (Anderson & Anderson 1985). Cycadophytes and ginkgolike remains also are found in the flora of the Parsora Beds of India (Lele 1962a,b; Rao & Lele 1963; Bose 1974), which is another example of the *Dicroidietum hughesii*. This fossil plant assemblage of India and South Africa lies within the dry to monsoonal subtropical paleoclimatic belt of the Gondwana supercontinent (Parrish 1990), whereas the *Dicroidietum zuberi* of southeastern Australia is within the humid cool temperate paleoclimatic region within the Antarctic circle (Anderson & Anderson 1985). The Culvida flora was probably near the ecotone between these two floristic regions. Its mix of species from north and south may be an indication of continuity of temperate woodlands through central Australia during the early Triassic.

Despite this regional variation in floras, the uniformity and low diversity of early Triassic floras is

impressive. It may be a lingering artifact of the Permian-Triassic life crisis. Extinctions of land plants have recently been shown to have been coeval with, and as severe as, the great dying of marine organisms (Retallack 1995). In addition, low diversity oligotrophic floras dominated by conifers and lycopods persisted for many millions of years after the Permian-Triassic boundary, with diversity of pteridosperm-dominated floras only attaining levels found in the Late Permian by Middle Triassic time with the *Dicroidium odontopteroides* flora of Gondwana and *Scytophyllum* flora of Laurasia. This low diversity oligotrophic interregnum was a time when there was no peat deposition anywhere in the world (Retallack *et al.* 1995). The record of land animals similarly shows a dramatic decline in diversity at the Permian-Triassic boundary followed by a cosmopolitan *Lystrosaurus* fauna of the early Triassic and then a diverse and provincial tetrapod fauna of the middle Triassic (Benton 1987). Similarly, in the sea, Early Triassic faunas were depauperate (Erwin 1994) and there are no known early Triassic reefs (Flügel 1994). These peculiarities of the early Triassic mark it as an unusual time. The big life crises in the history of life may indeed change the rules, making difficult the application of uniformitarianism in interpreting the past.

Systematic palaeobotany

CLASS LYCOPSIDA

ORDER ISOETALES

GENUS *PLEUROMEIA* Corda for Germar 1852

Pleuromeia dubia (Seward) comb nov

Holotype. Stem cast (South African Museum 13727)

Type locality. Alcock's Quarry, near Aliwal North, South Africa; Burgersdorp Formation: Early Triassic (Anderson & Anderson 1985).

Description. The single leaf found at Culvida Soak (F9155, Fig 2E) is very similar to "*Cylomeia undulata*" (White 1981), but that name is unsuitable for a variety of reasons. The holotype of "*C. undulata*" is a fossil leaf identical to the Culvida fossil, called "*Taeniopteris undulata*" by Burges (1935). Its lateral wrinkles are probably due to compression or drying of a thick and fleshy lycopsid leaf (White 1981). I could not make out a supposed "very delicate" lateral venation spaced at "30 per cm" noted by Burges (1935) as evidence of cycadophytic affinities on either the type or Culvida material. Kimura (1959) was evidently not aware of this species when he erected the name *Taeniopteris undulata* for some quite different cycadophyte leaves of Upper Jurassic age in Japan. Confusion is now removed by the discovery of "*Cylomeia undulata*" leaves attached to lycopsid stems of "*Gregicaulis dubius*" in both the Newport Formation near Sydney Australia (Retallack 1973) and the Burgersdorp Formation near Aliwal North, South Africa (Anderson & Anderson 1985). Associated oval sporophylls with rounded tips have been found both in South Africa (Anderson & Anderson 1985) and in the Culvida Sandstone (White & Yeates 1976, Pl 12, Figs 44,45). Pleuromiacean lycopsids are best identified according to reproductive structures



Figure 2. Fossil fern, lycopsid and seed ferns from Culvida Soak; A, B, *Cladophlebis carnei* (F9160); C, G, *Dicroidium narrabeenense* (F9154, F9149 respectively); D, *Dicroidium hughesii* (F9155); E, *Cylomeia undulata* (F9155); F, *Dicroidium zuberi* (F9144).

(White 1981; Sadovnikov 1982; Dobruskina 1985), and these sporophylls leave little doubt that "*Gregicaulis*" is a junior synonym of *Pleuromeia*, here taken in a stricter than usual sense. *Pleuromeia dubia* was originally described as "*Stigmatodendron dubium*" by Seward (1908), but that genus is based on remains of a Carboniferous arborescent lycopsid from Russia.

Distribution. *Pleuromeia dubia* is known from the Burgersdorp Formation of South Africa (Anderson & Anderson 1985) and the Newport Formation (Retallack 1973; White 1981) and Camden Haven Claystone (Holmes & Ash 1979) of southeastern Australia, all of late Early to early Middle Triassic age.

CLASS PTEROPSIDA

ORDER & FAMILY INCERTAE SEDIS

GENUS *CLADOPHLEBIS* Brongniart emend

Frenguelli 1947:12

Cladophlebis carnei Holmes & Ash 1979 (Figs 3A,B)

Holotype. Australian Museum partial frond F59425

Type locality. Camden Head near Laurieton, NSW; Camden Haven Claystone; late early to early Middle Triassic.

Description. One of the fossils from Culvida Soak (F9160, Fig 2A,B) has the characteristic falcate pinnules and singly forked lateral venation of this species. It is most similar to *Cladophlebis oblonga* Halle, which has somewhat blunter, wider pinnules and thicker rachis (Frenguelli 1947).

Affinities. Similar leaves are found with sporangia similar to those of *Asterotheca* in the Newport Formation of NSW (Retallack 1973, 1980a), Estratos del Alcázar of Argentina (Menendez 1957), and Burgersdorp Formation of South Africa (Anderson & Anderson 1985), so these leaves were probably marattialean ferns.

Distribution. In addition to the type locality, this species is known from the early Triassic Newport Formation near Sydney, NSW (Retallack 1973, 1980a), Estratos del Alcázar near Hilario, Argentina (Menendez 1957), Burgersdorp Formation near Aliwal North, South Africa (Anderson & Anderson 1985), and Middle Triassic Gunnee Beds near Delungra, N.S.W. (Bourke *et al.* 1977).

GENUS *CHIROPTERIS* Kurr emend Rühle von Lilienstern 1931:273

Chiropteris whitei sp nov (Figs 3F-J,4C)

1961 *Ginkgoites antarctica* White p 302, Pl 3, Fig 5

Holotype. The most complete leaf (F9158, Fig 4C), whose outline is reconstructed in Fig 3G.

Type locality. Culvida Soak, Canning Desert, Western Australia; Culvida Sandstone, late Early to early Middle Triassic.

Diagnosis. Reniform leaves, width about 40 mm (25-60 mm), with a petiole at least 12 mm long attached at a wide angle to the blade; leaf margin crenate and slightly recurved; venation fine, evenly radiating from petiole,

anastomosing and dichotomising throughout the leaf, obscured by interveinal woody striae.

Derivation. The specific epithet is from Mary E White, who pioneered paleobotanical studies of the Canning Basin and other outback Australian localities.

Comparison. Although very similar to the leaves of *Ginkgo*, these fossils (F9150, F9156-9) differ in their anastomosing venation (Fig 4C), reniform shape (Fig 3G) and angle of insertion of the petiole (reconstructed in Fig 3I). The venation is obscured by abundant woody interveinal striae, and the leaf texture was stiff enough for the conical shape of the leaf blade and a slightly recurved margin to have resisted compaction (Fig 4C). The leaf was also wrinkled in broad zones corresponding to growth ridges. These also are differences from ginkgoalean leaves.

There are two distinctive kinds of species within the genus *Chiropteris* now that the apetiolate woody species have been removed to *Ginkgophytopsis* (by Retallack 1980b). One group includes *Chiropteris zeilleri* (Seward 1903), and *C. barrealensis* (Frenguelli 1942) and has palmate, flabellate leaves with widely spaced clear venation, characteristically without anastomosis between the central two veins, unlike *C. whitei*. Another group includes the type species *Chiropteris lacerata* (Rühle von Lilienstern 1931), *C. reniformis* (Kawasaki 1925), *C. kawasakii* (Kon'no 1939) and *C. harrisii* (Archangelsky 1960). These are conical, circular or reniform leaves with dense venation and common interveinal striae, like *C. whitei*. Of these species, *C. whitei* is most like *C. harrisii*, which differs in being twice the size, with wider lateral lobes. These species have much less developed lateral lobes than in *C. reniformis* and *C. kawasakii*. The type species of the genus, *C. lacerata* is more strongly conical, cutinized and lignified than *C. whitei*, and has in addition a lamina more dissected and lobes not extending backward past a right angle to the petiole.

Affinities. Affinity of these plants with ginkgoaleans has long been thought unlikely, and Rühle von Lilienstern (1931) proposed that the type species was a dipteridacean fern on the basis of its reflexed conical leaf shape, anastomosing venation and supposed sori. These latter look more like insect domatia (of Stace, 1965) than sori and the details of the venation are quite unlike the nearly square meshes of typical dipteridacean ferns. Another possibility is that these are progymnosperms allied to *Archaeopteris* as suggested for the similar *Ginkgophytopsis* by Retallack (1980b). A possible progymnosperm sporangial axis has been found in a New Zealand locality yielding *Ginkgophytopsis* (Pole & Raine, 1994), but both *Ginkgophytopsis* and *Chiropteris* remain problematic.

CLASS PTERIDOSPERMOPSIDA

FAMILY CORYSTOSPERMACEAE Thomas 1933

GENUS *DICROIDIDIUM* Gothan emend. Townrow 1957:26.

Dicroididium hughesii (Feistmantel) Lele 1962a (Figs 2D, 4A)

Remarks. This large unipinnate leaf (F9155) was evidently forked, as two rachides converge on the slab (Figs



Figure 3. Fossil seed ferns and problematica from Culvida Soak; A, *Lepidopteris madagascariensis* (F9148); B-D, *Dicroidium zuberi* (F9151, F9143, F9152 respectively); E, *Umkomasia* sp indet (F9147); F-J, *Chiopteris whitei* (F9159, F9158, F9150, reconstructed leaf, F9156 respectively).

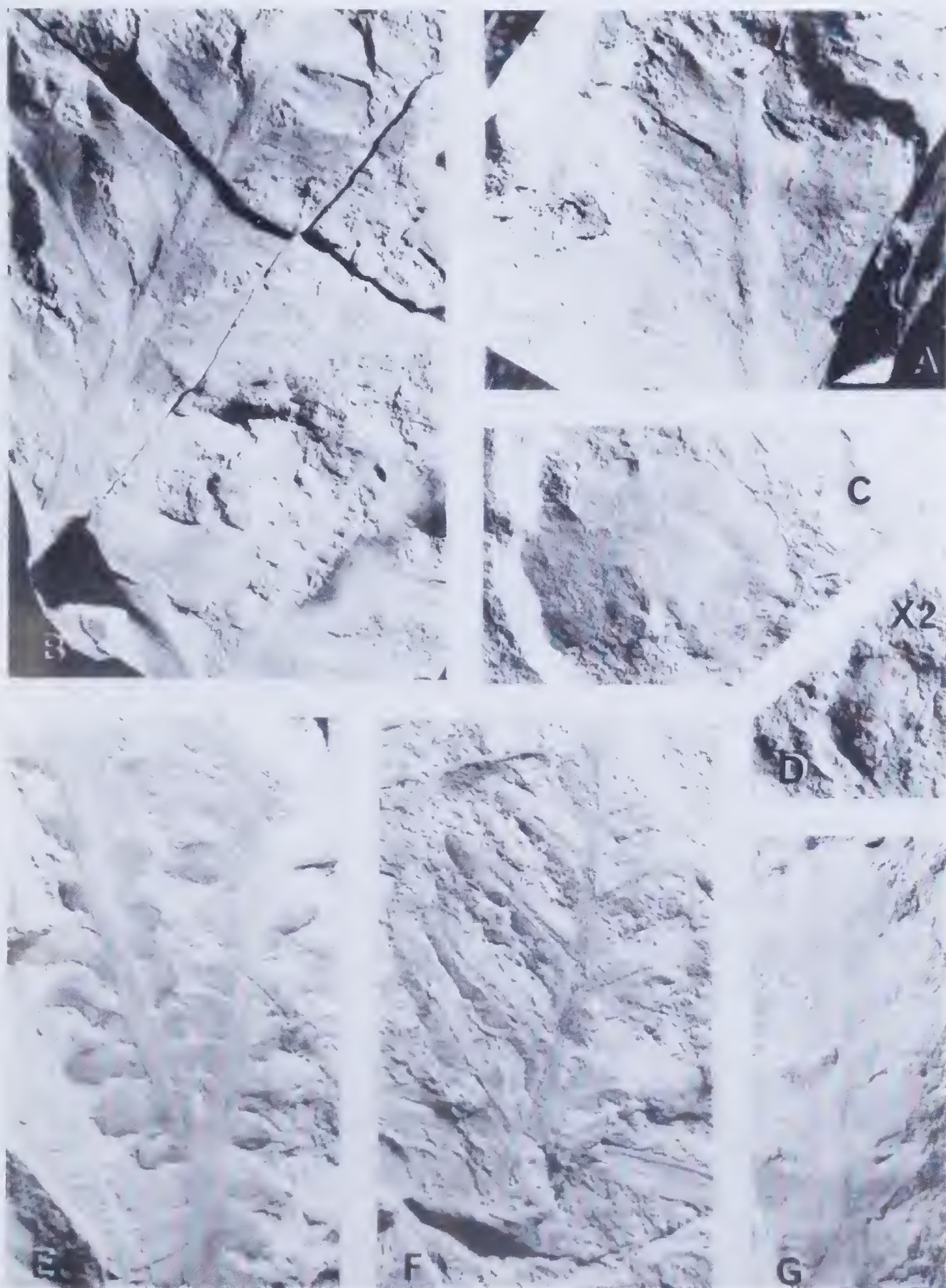


Figure 4. Fossil seed ferns and problematica from Culvida Soak: A, G, *Dicroidium narrabeenense* (F9154, F9149 respectively); B, *Dicroidium hughesii* and *Pleuromeia dubia* (F9155); C, *Chiropteris whitei* (F9158); D, *Unkoniasia* sp (F9147); E, F, *Dicroidium zuberi* (F9152, F9143 respectively).

2D, 4A). It shows veins clearly, as well as basiscopic lobes to the pinnae that are the hallmarks of this species, distinguishing it from the otherwise similar *Dicroidium narrabeenense* Jacob & Jacob (1950). *Dicroidium eskense* is another comparable leaf distinguished by asymmetric pinnae, but in this case due to a deep acroscopic sinus in the pinnae (Retallack 1977).

Distribution. *Dicroidium hughesii* is well known from the Parsora Beds of India (Lele 1962a) and the Burgersdorp Formation of South Africa (Anderson & Anderson 1985). In both places, it is the dominant taxon, whereas only a few specimens were found at Culvida Soak [including material of White (1961) and White & Yeates (1976)].

Dicroidium narrabeenense (Walkom) Jacob & Jacob 1950 (Figs 2C-D, 4B, G)

Remarks. This species is represented by two specimens (F9149, F9153-4). It is here interpreted in the broad sense of Anderson & Anderson (1983), who included bipinnatifid remains referred to "*Dicroidium australe*" by Jacob & Jacob (1950) as well as smaller leaves (Fig 2G) that formerly would have been referred to "*Dicroidium lancifolium*". However it has long been recognized that "*D. lancifolium*" is an extreme variant of *D. odontopteroides* (Retallack 1977), as well as of *D. narrabeenense*. The leaves similar to "*D. lancifolium*" associated with *D. odontopteroides* have pinna bases separated at the rachis, and are thin in texture, with clear venation, and thin cuticles with laterocytic stomata (Anderson & Anderson 1983), whereas leaves similar to "*D. lancifolium*" associated with *D. narrabeenense* have confluent to overlapping pinna bases, are so thick that veins are difficult to see, and have thick cuticles with cyclocytic stomata (Jacob & Jacob 1950; Retallack 1973). Although cuticles cannot be prepared from the Culvida Soak specimen similar to "*D. lancifolium*", it was thick with confluent pinna bases as in *D. narrabeenense*.

Distribution. *Dicroidium narrabeenense* has been found in the Newport Formation near Sydney (Retallack 1973, 1980a) and the Camden Head Claystone near Laurieton, NSW (Holmes & Ash 1979), both late Early to early Middle Triassic (Scythian-Anisian). Comparable leaves also have been found from the Parsora Beds of India (as "*Dicroidium odontopteroides*" of Lele 1962a), of the same age (Anderson & Anderson 1983).

Dicroidium zuberi (Szajnocha) Archangelsky 1968 (Figs 2F, 3B-D, 4E-F)

Remarks. This is a common, widespread and polymorphic species. One of the Culvida specimens is most like *D. zuberi* var *papillatum* (Townrow) Retallack (1977: F9145) which has rhomboidal pinnules, but most of them are like *D. zuberi* var *sahnii* (Seward) Retallack (1977: F9143-4, F9146-7, F9149-50, F9152) which has rounded pinnules that tend to coalesce into lobed outer pinnae. These varieties were intended as form-taxa. The frond size of the Culvida specimens is small and compact for this species (Retallack 1977, 1980a).

Artabe (1990) has proposed that Frenguelli's genus *Zuberia* be resurrected for bipinnate *Dicroidium* leaves

with rachis pinnules, so that the varieties of Retallack (1977) would become species of *Zuberia*. Many of these bipinnate *Dicroidium* leaves do have distinctive cyclocytic stomata (Townrow 1957; Anderson & Anderson 1983), but some have laterocytic stomata and cuticles otherwise identical to those of *Dicroidium odontopteroides* (Townrow 1957). Until more information is available on cuticular and other distinctive characters of the type Argentinian specimens of *Zuberia*, that genus is maintained as a junior synonym of *Dicroidium*.

Distribution. Very similar leaves to *D. zuberi* var *papillatum* have been found in the Newport Formation near Sydney, NSW (Retallack 1973, 1980a) and in the Erskine Sandstone at Derby, Western Australia (Antevs 1913; Townrow 1957). *Dicroidium zuberi* var *sahnii* is known from the Newport Formation near Sydney, NSW (Retallack 1973, 1980a) and from the Parsora Beds of the South Rewa Basin, India (Seward 1932; Lele 1962a).

GENUS *UMKOMASIA* (Thomas) emend Holmes 1987: 166.

Umkomasia sp indet (Fig 2E)

Remarks. This single cupule (F9147) is 8.3 x 6.2 mm in size, and appears identical to the more complete branching group of three cupules from Culvida Soak illustrated by White & Yeates (1976, Pl 13, Fig 49). They appear to have three or four cupule lobes. They thus have fewer lobes and are smaller in size than early Triassic *Umkomasia feistmantelii* (Holmes & Ash) Holmes (1987) and larger in size with more cupule lobes than other described species of middle and late Triassic age (Thomas 1933; Holmes 1987).

Distribution. The Culvida specimens are most like those associated with the type material of *Dicroidium zuberi* from the early Triassic Barreal Formation, near Barreal, Argentina (Frenguelli 1944a).

FAMILY PELTASPERMACEAE Thomas 1933

GENUS *LEPIDOPTERIS* Schimper emend Townrow 1956; 4.

Lepidopteris madagascariensis Carpentier 1935 (Fig 2A)

Remarks. Only one specimen was found (F9148), but it shows the distinctive rachis-pinnules, rounded pinnule apices and a conspicuous median ridge to the rachis that is distinctive for this species. The current specimen lacks the rounded pinnules and large blisters on the rachis of the Permian species *Lepidopteris stuttgardiensis* and *L. martinsii*, but has less pointed and lobed pinnules than the middle Triassic species *L. stormbergensis* (Townrow 1966). Its pinnules are not so large or coalescent as in *L. brownii* or *L. africana* (Anderson & Anderson 1989). Constricted pinnule bases distinguish *L. langloensis* (Anderson & Anderson 1989).

Distribution. This species has been found in the Hawkesbury Sandstone and Newport Formation near Sydney, NSW (Townrow 1966), the Camden Haven Claystone near Laurieton, NSW (Holmes & Ash 1979), and the Burgersdorp Formation near Aliwal North, South Africa (Anderson & Anderson 1985), all of late

Early to early Middle (Scythian-Anisian) age. The type material was found at Amboriky in the early Triassic bed 3 of the Sakamena Group of Madagascar (Carpentier 1935).

Acknowledgements: I thank R J Paten of Mines Administration Pty Ltd for sending these fossils and R E Gould for notifying me about them. A N Yeates, J E Gorter and M E White offered useful discussion on Canning Basin geology and paleontology. J H Lord of the Western Australian Geological Survey provided a repository for the specimens. Research was funded by a Commonwealth Postgraduate Award and NSF grant OPT9315228.

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New Pleistocene and Holocene stratigraphic units in the Yalgorup Plain area, southern Swan Coastal Plain

V Semeniuk

21 Glenmere Road, Warwick WA 6024

Received June 1995; accepted November 1995

Abstract

Within the area of Yalgorup Plain (amended from the Yoongarillup Plain) between Mandurah and Bunbury, there are a variety of fossiliferous limestone, aeolian limestone, and quartz sand units. Three new Pleistocene formations are recognised: the Tims Thicket Limestone, the Myalup Sand, and the Kooallup Limestone. These formations, previously part of the Tamala Limestone, underlie distinct Pleistocene landforms and comprise distinct shore-parallel systems formed by coastal progradation, interrupted by subaerial unconformities. They represent sedimentation during the Pleistocene, which was dominated by cusped forelands, barriers, and wave-built platforms.

The western edge of the Yalgorup Plain is bordered by Holocene barrier dunes which are a geomorphic extension of the Leschenault Peninsula barrier. Various Holocene formations underlie the barrier in the Yalgorup region. Generally, they can be assigned to the Safety Bay Sand, Becher Sand, Bridport Calcilutite, and Leschenault Formation, and to the Preston Beach Coquina, a new unit formally defined in this paper. Four types of large-scale standard Holocene stratigraphic sequences can be recognised in this region: Type 1, prograded bank, beach, beachridge sediments; Type 2, prograded shoreface to beachridge sediments; Type 3, retrograded barrier dune sediments overlying estuarine lagoonal sediment; and Type 4, retrograded barrier dune sediment unconformable on Pleistocene sediment. These standard sequences can be used to help unravel the Holocene history of the barrier dunes in the Yalgorup area, and specifically between Preston Beach and the Bouvard Reefs.

Introduction

The western part of the Swan Coastal Plain between Mandurah and Bunbury contains Pleistocene limestone (McArthur & Bettenay 1960; Playford *et al.* 1976), linear wetlands and estuarine lagoons, and a shore-parallel Holocene barrier dune system (Searle & Semeniuk 1985; Semeniuk 1985). Within this area is the Yalgorup Plain (amended here from the Yoongarillup Plain), a Pleistocene to Holocene surface developed on a variety of fossiliferous limestone, aeolian limestone, and quartz sand. Previous drilling in this area was conducted by Commander (1988).

Recent research has delineated a range of new Pleistocene to Holocene stratigraphic units in this area, which are described in this paper. Recognition of these new units has provided a tool to unravel the local Pleistocene and Holocene coastal history, as described in Semeniuk (1995a,b). Stratigraphic and geomorphic patterns derived from the Pleistocene terrain in the region show that there are distinct shore-parallel tracts of Pleistocene landforms that developed by coastal progradation, interrupted by subaerial unconformities. Sedimentation was dominated by narrow beachridge plains and cusped forelands (Semeniuk 1995a). Defining a new Holocene stratigraphic unit in the region has also aided in the recognition of four key stratigraphic sequences that help unravel coastal history.

Stratigraphic data for this paper are from drill holes, road cuts, quarries and excavations. Description of stratigraphy and drilling transects, apart from those provided for the type sections in this paper, are presented more fully by Semeniuk (1995a,b).

Amendment of the Yoongarillup Plain to Yalgorup Plain

There has been a problem with the concept, nomenclature and application of the term Yoongarillup Plain in the Mandurah-Bunbury area (McArthur & Bartle 1980; Semeniuk 1990). Originally the term "Yoongarillup" was used to denote a quartz sand underlying a plain developed on fossiliferous limestone near Busselton, and named after locality in that area (McArthur & Bettenay 1958). Through application in mapping, the term "Yoongarillup" eventually came to encompass a wider range of landforms and soils. The term Yoongarillup Plain was first formally used as a landform/soil unit describing a melange of near-coastal plains and flats between Mandurah and Bunbury (McArthur & Bartle 1980) that included coastal plains underlain by fossiliferous limestone, supratidal to tidal estuarine flats, and geomorphically degraded Quindalup Dunes. An earlier attempt was made to rationalise the use of the term firstly, by excluding the terrain of Quindalup Dunes and estuarine-related flats from the definition, and secondly by restricting the term to refer to the genetically distinct fossiliferous limestone plains

formed by Pleistocene marine progradation that are restricted palaeogeographically to the Mandurah-Bunbury area (Semeniuk 1990). At the time of this first amendment (Semeniuk 1990), the opportunity also existed to rectify the name, but this was not done. The term "Yoongarillup", deriving from the locality of Yoongarillup, south of Busselton, should refer to features in that region, and not to those restricted to the coastal tract between Bunbury and Mandurah. At present, following extended usage from the Busselton area into the Mandurah-Bunbury area by McArthur & Bartle (1980), and later amendment by Semeniuk (1990), the term "Yoongarillup Plain" now refers to a coastal plain quite removed from its origin. Following the results that clarify the Pleistocene palaeogeography in this region (Semeniuk 1995a), I propose that the situation be now rectified: firstly; that the term Yoongarillup Plain be restricted to the Busselton area; and secondly, that the term "Yalgorup Plain", derived from the local region, be applied to the set of coastal landforms that are palaeogeographically restricted to the Mandurah-Bunbury region. In this way, two genetically and geographically distinct plains will have different names.

The Pleistocene palaeogeographic system, and stratigraphic units within the Yalgorup Plain and adjacent systems

The Yalgorup Plain

The Yalgorup Plain is long and narrow, some 60 km long and 5–6 km wide (Fig 1), and is underlain by fossiliferous limestone, aeolian limestone and quartz sand. Though generally of low relief and undulating, there is local relief of 5–10 m (and up to 15 m) in the form of either calcarenitic aeolianite ridges or quartz sand ridges. The Plain is bordered to the east by a prominent ancestral hinterland ridge (the Mandurah-Eaton ridge; Semeniuk 1995a) that is a linear, moderately high (on average 20–40 m high, locally up to 70 m high, and itself on average some 20 m higher than the Yalgorup Plain), and 3–4 km wide, extending in a north-south direction for 90 km from Mandurah to Eaton (Fig 1), with a slight concavity in its form on the western margin. The junction of this ridge with the Yalgorup Plain is sharp, with the ridge descending steeply down to the Plain. The Mandurah-Eaton ridge is composed of Pleistocene aeolian quartz sand and aeolian limestone but has variable stratigraphy from south to north. To the south, it is mainly quartz sand and lesser limestone (Eaton Sand, Semeniuk 1983), with limestone occurring as aeolianite lenses (Semeniuk & Glassford 1987). To the north, limestone is more common. Even where limestone dominates, the ridge is mantled by yellow quartz sand. The Plain is bordered to the west by a Holocene coastal barrier aeolian ridge (the Leschenault-Preston barrier), or by Holocene estuarine lagoonal deposits.

Offshore from the Yalgorup Plain, the nearshore shelf is mostly an unconformity surface cut into Pleistocene limestone, with veneers of quartz sand or Holocene sediment (Semeniuk & Meagher 1981; Searle &

Semeniuk 1985). Locally, particularly to the north of the study area, remnant shore-parallel ridges of Pleistocene limestone form discontinuous rocky reefs and islands (the Bouvard Reefs). Another line of former reefs, the Buffalo Reefs, occurs buried under Holocene dunes to the south (Semeniuk 1995a). Generally, there are no prominent limestone ridges or rocky reefs, buried or otherwise, in the central part of the area.

The age of the Plain is concluded to be Pleistocene, for the following reasons; 1, the formations that underlie the plain abut or overlie other units in the area are generally conceded to be Pleistocene in age (e.g. the Bassendean Sand, and the yellow sand and limestone that underlies the Mandurah-Eaton Ridge); 2, radiocarbon ages for the limestones at various sites returned ages >30–40,000 years.

Pleistocene lithologies

Ten types of sedimentary rock and sediment in the Pleistocene sequences occur in this region. These are (limestone terminology follows Dunham 1962):

1. Shelly/bioturbated calcarenite: fine to medium grained, bioturbated to structureless, skeletal quartz grainstone, with abundant calcareous algae and invertebrate skeletons. Shell locally present and randomly oriented by bioturbation;
2. Bioturbated foraminiferal calcarenite: fine to medium sand grainstone of calcareous algae, invertebrate skeletons, quartz, shell grit, whole molluscs, and abundant granule-sized foraminifera (*Marginopora*); bioturbation consists of vertical burrows 3–4 cm diam, penetrating downwards for 50–75 cm, otherwise bioturbation shows general swirling;
3. Laminated and cross-laminated marine calcarenite: medium grained skeletal quartz grainstone, generally without shell beds; conspicuously laminated, cross-laminated and trough-bedded;
4. Laminated to cross-laminated beach calcarenite: skeletal quartz grainstones, with variable structure and texture, but forming a set vertical sequence, usually over 2.0–2.5 m. Mollusc shells present (*Donax* most common); sedimentary structures and two diagnostic cephalopods distinguish four subfacies (Semeniuk & Johnson 1982) – lower part is trough-bedded, medium to coarse grained, with local shells, middle zone is medium to coarse grained, with oriented shell, and low inclined cross-lamination, then there is medium grained calcarenite, with bubble-sand structures, and upper part is crudely layered to bioturbated to structureless, medium to coarse grained, with diagnostic cephalopods *Sepia* and *Spirula*;
5. Cross-laminated to structureless calcarenitic aeolianite: large scale cross-laminated to structureless fine to medium grained skeletal quartz grainstone; cross-lamination sets 2–5 m high; calcrete rhizoconcretions and pipes common;
6. Calcreted limestone: this limestone is mainly calcrete in sheet-like form, 20–30 cm thick, or massive, within and on top of the parent limestone, or coating

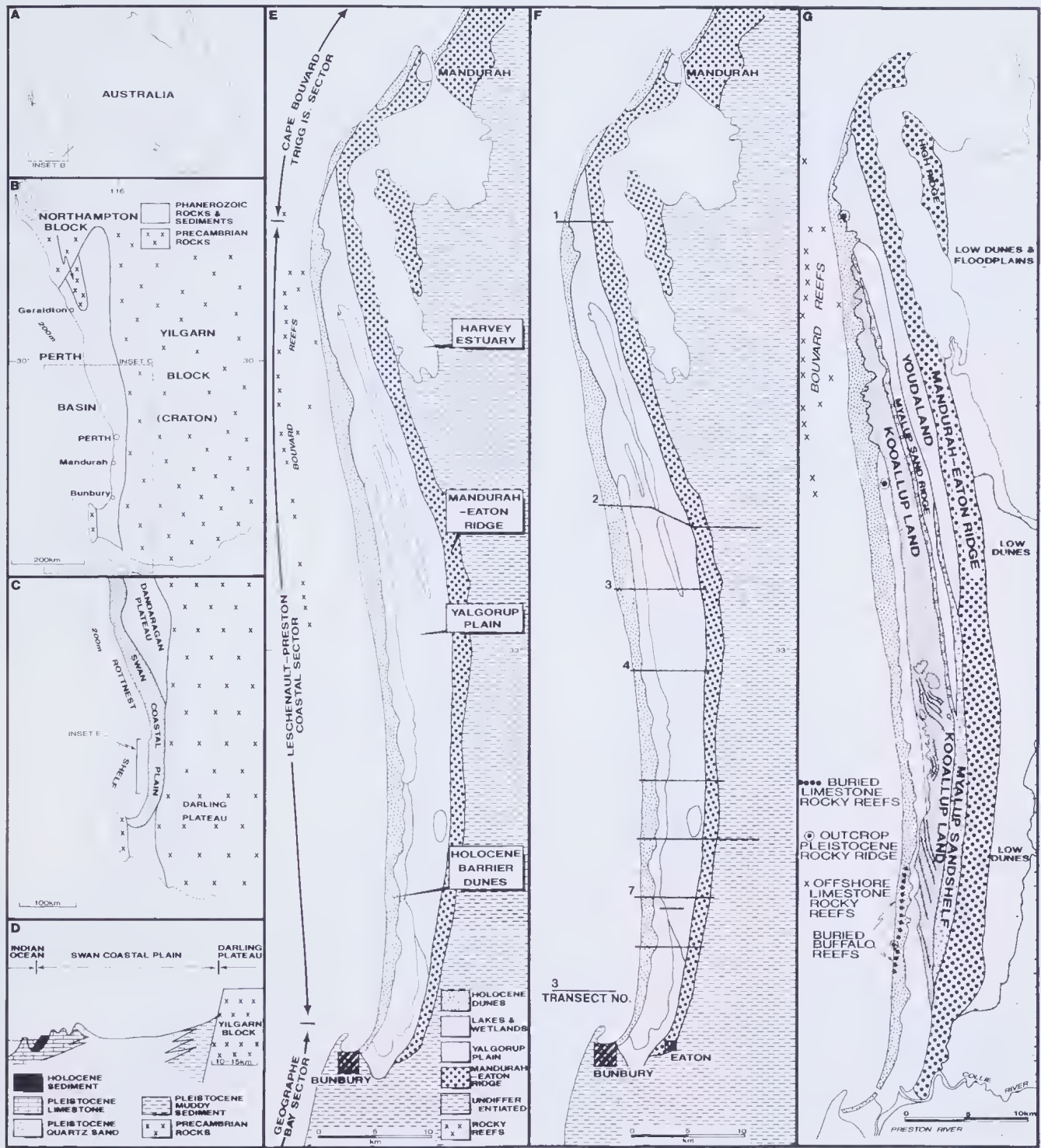


Figure 1. A, B, C & D: Location of study area in southwestern Australia in relationship to regional geology and geomorphology. E: Location of the Holocene Quindalup Dunes, Yalgurup Plain, and offshore reefs, and location of drill sites and quarries for type sections. F: Location of study transects (Transects 1-4 & 7 are presented in Figure 2; the full data including the un-numbered transects are presented in Semeniuk 1995a). G: Map of the Pleistocene geomorphic units (landforms) on the Yalgurup Plain.

- pipes; lateral and vertical relationships and gradations, and palimpsest grains and textures indicate parent lithology was aeolianite;
7. Indurated, bored limestone: limestone varies from aeolianite to shelly limestone, and may also be calcreted; key features are induration by calcite cements (fine grained calcite, sparry calcite, calcrete), borings and pot-holes; borings are 1 cm diameter or less; limestone surface may be fissured, with local pot-holes some 10-30 cm diameter, and veneered with rounded limestone gravel and shells of *Ninella*, *Marmarstoma*, *Littorina*, limpets, barnacles;

8. Shelly calcilutite: structureless lime mudstone to skeletal lime mudstone;
9. Quartz sand: yellow, grey, or white, medium grained, and well to poorly sorted; grains mostly quartz, with some feldspar and minor heavy minerals; quartz sand in this area is largely structureless (cf. Glassford & Semeniuk 1990); and
10. Shelly terrigenous mud: dark grey, structureless terrigenous mud with estuarine shells.

Some general features about these lithologies are noted here. All limestones are generally white, cream, tan to buff in colour. Grainstones are weakly to strongly cemented by sparry calcite, depending on location relative to the water table. Most limestones also are variably weakly indurated by calcrete, and additionally may be stained by iron oxides. Molluscs in the fossiliferous limestones (Table 1) are typically assemblages from seagrass bank environments (cf. Logan *et al.* 1970; Semeniuk & Searle 1985; Semeniuk 1995a). Calcreted limestone is a rock type best developed at unconformity surfaces, and indicates major subaerial exposure. Indurated, bored limestone (often with a gravel veneer of limestone lithoclasts and shells) is generally a micrite- or calcrete-indurated surface that had been exposed as a shore platform or hardground in the submarine shelf environment; this type of limestone has analogues in the Holocene and also indicates a major unconformity.

Pleistocene formations

Pleistocene limestones and quartz sand form distinct tracts of terrain on the Yalgorup Plain. Three new formations are described here to facilitate interpretation of the regional Quaternary history and palaeogeography. Previously, the limestone units in this area were referred to the Tamala Limestone, but they can be identified readily as distinct units by their lithology, stratigraphy and geography. They are lithologically distinct from the Tamala Limestone at its original location (Logan *et al.* 1970), at its type section (Playford & Low 1972), and from the calcarenitic aeolianite regarded as Tamala Limestone in the central Swan Coastal Plain of the Perth Regional area (Fairbridge 1953; Klenowski 1976; Gozzard 1983, 1986). Pleistocene limestones that comprise the offshore limestone ridges and the deeper sections of the Quaternary profile are left undifferentiated at present.

The new Pleistocene formations are:

3. Kooallup Limestone: a Late Pleistocene shoaling sequence of submarine, beach and aeolian calcarenites;
2. Myalup Sand: quartz sand, mostly grey to white, generally sandwiched between the Tims Thicket Limestone and Kooallup Limestone;
1. Tims Thicket Limestone: a shoaling sequence of submarine, beach and aeolian calcarenites deposited earlier in the Pleistocene.

The features of these formations are summarised in Table 2. The stratigraphy and relationships between the units are shown in Figures 2 & 3.

Table 1

List of molluscs in the Tims Thicket & Kooallup Limestones

BIVALVIA:

<i>Anodontia perplea</i>	<i>Irus distans</i>
<i>Brachidontes ustulatus</i>	<i>Macra australis</i>
<i>Callucina lacteola</i>	<i>Macra matthewi</i>
<i>Chlamys asperimus</i>	<i>Mysella</i> sp
<i>Chionery cardioides</i>	<i>Saccostrea cucullata</i>
<i>Divalucina cumingi</i>	<i>Paphies cuneata</i>
<i>Dona francisensis</i>	<i>Pinna</i> sp
<i>Electroma georgiana</i>	<i>Tawera coelata</i>
<i>Eucrassatella</i> sp	<i>Tawera lagopus</i>
<i>Glycymeris strialularis</i>	<i>Tellina tenuilrata</i>
<i>Gomphina undulosa</i>	<i>Thraciopsis subrecta</i>
<i>Hemidona chapmani</i>	<i>Wallucina cf jacksoniensis</i>

GASTROPODA:

<i>Acteocina</i> sp	<i>Mitrella austrina</i>
<i>Analda monilifera</i>	<i>Mitrella menkeana</i>
<i>Amblychilepas oblonga</i>	<i>Naccula punctata</i>
<i>Astrarium squamiferum</i>	<i>Natica</i> sp
<i>Bedevea paivae</i>	<i>Notocochlis gualteriana</i>
<i>Bittium granarium</i>	<i>Notomella bajula</i>
<i>Bulla quoyii</i>	<i>Oliva australis</i>
<i>Calyptraea calyptraeformis</i>	<i>Parcanassa</i> sp
<i>Cantharidus lepidus</i>	<i>Phasianella australis</i>
<i>Cantharidus irisodontes</i>	<i>Phasianella solida</i>
<i>Cantharidus</i> sp	<i>Phasianella ventricosa</i>
<i>Clanculus</i> sp	<i>Phasiatrochus bellulus</i>
<i>Collisella onychitis</i>	<i>Polinices conicus</i>
<i>Cominella tasmanica</i>	<i>Proterato sulcerato</i>
<i>Conus anemone</i>	<i>Pyrene scripta</i>
<i>Dicathais orbita</i>	<i>Pyrenidae pseudomycla</i>
<i>Drupa</i> sp	<i>Symnola</i> sp
<i>Ettiminolia vitiliginea</i>	<i>Thalotia conica</i>
<i>Gibbula lehmanni</i>	<i>Thalotia lehmanni</i>
<i>Gibbula preissana</i>	<i>Thalotia pulcherrima</i>
<i>Haminocia brevis</i>	<i>Thalotia chlorostoma</i>
<i>Hipponi conicus</i>	<i>Turbo intercostalis</i>
<i>Hipponi foliaceus</i>	<i>Tanea sagittata</i>
<i>Leiopyrga octona</i>	<i>Veillum marrowi</i>
<i>Mangelia</i> sp	<i>Zafra vercoi</i>

Most identifications based on standards identified by G W Kendrick (Western Australian Museum) as cited by Semeniuk & Searle (1985); supplementary identifications from Roberts & Wells (1981) and Wells & Bryce (1985).

All molluscs listed, except for the gastropod *Parcanassa* are also present in Holocene seagrass assemblages, cf Semeniuk & Searle (1985)

Tims Thicket Limestone

Definition and characteristics: The Tims Thicket Limestone is a Pleistocene fossiliferous and non-fossiliferous calcarenite cropping out along the eastern Yalgorup Plain. Its lower to middle part is fossiliferous marine, and its uppermost part is aeolian.

Derivation of name: Tims Thicket area in the northern Yalgorup National Park.

Type section: A disused quarry at 32°39'06" 115°37'36", along Tims Thicket Road.

Distribution: The formation is restricted to the Yalgorup Plain area, and crops out almost along the entire length of the eastern part of the Plain (Fig 1). It also is intersected in cores underlying Holocene units.

Table 2

Limestone members in Pleistocene formations in the Yalgorup coastal area

FORMATION	MEMBER	LITHOLOGY	COMMENTS
KOOALLUP LIMESTONE	LAKESIDE MEMBER	cross-laminated to structureless, fine and medium calcarenite	aeolianites
	BELLEVUE MEMBER	white to cream shelly / bioturbated calcarenite, laminated cross-laminated shelly calcarenite/coquina, laminated to crosslaminated beach calcarenite	submarine to beach zone facies
	SPRINGHILL MEMBER	calcilutite and shelly calcilutite	submarine basin facies
TIMS THICKETT LIMESTONE	WHITE HILL ROAD MEMBER	cross-laminated to structureless, fine and medium calcarenite	aeolianites
	CLIFTON DOWNS MEMBER	white to cream shelly / bioturbated calcarenite, bioturbated foraminiferal limestone, laminated cross-laminated marine calcarenite laminated to cross-laminate beach calcarenite	submarine to beach zone facies

Table 3

Description of Holocene stratigraphic units¹ in the Yalgorup coastal area

SEDIMENT UNIT	STRUCTURE	LITHOLOGY	HOLOCENE DEPOSITIONAL ENVIRONMENT
Safety Bay Sand (aeolian facies)	large scale cross laminated to structureless	white, cream, orange fine and medium sand	dune
Safety Bay Sand (beach facies)	laminated to bedded; seaward sloping layers	white, cream, yellowish medium and coarse sand and shelly sand	beach
Preston Beach Coquina	bedded to crudely layered	white, cream, yellowish, & tan shell beds, shell grit, shelly sand, and coarse to medium sand	subtidal shoreface to beach
Becher Sand	structureless, bioturbated crudely layered	grey sand and shelly sand; shells from seagrass assemblage	subtidal seagrass bank
Bridport Calcilutite	structureless to bioturbated; shell layers	grey calcilutite and shelly calcilutite	deep subtidal basin
Leschenault Formation	structureless, bioturbated, crudely layered	grey sand, mud, muddy sand, locally shelly; estuarine shells	estuarine sand and mud flats

¹ Data from Semeniuk (1983), Semeniuk & Searle (1985, 1987), and this paper.

Thickness and geometry: At the type section, the formation has been logged as 9.1 m thick. Regionally, the unit is a ribbon to wedge, some 60 km long, up to 5 km wide and 5–10 m thick.

Lithology: The sequence of limestone at the type section (from 1 at the base to 5 at the top) is:

- cross-laminated to structureless calcarenitic aeolianite: 2.0 m thick;
- laminated to cross laminated beach calcarenite: 2.0 m thick;
- laminated and cross laminated marine calcarenite: 1.3 m thick;

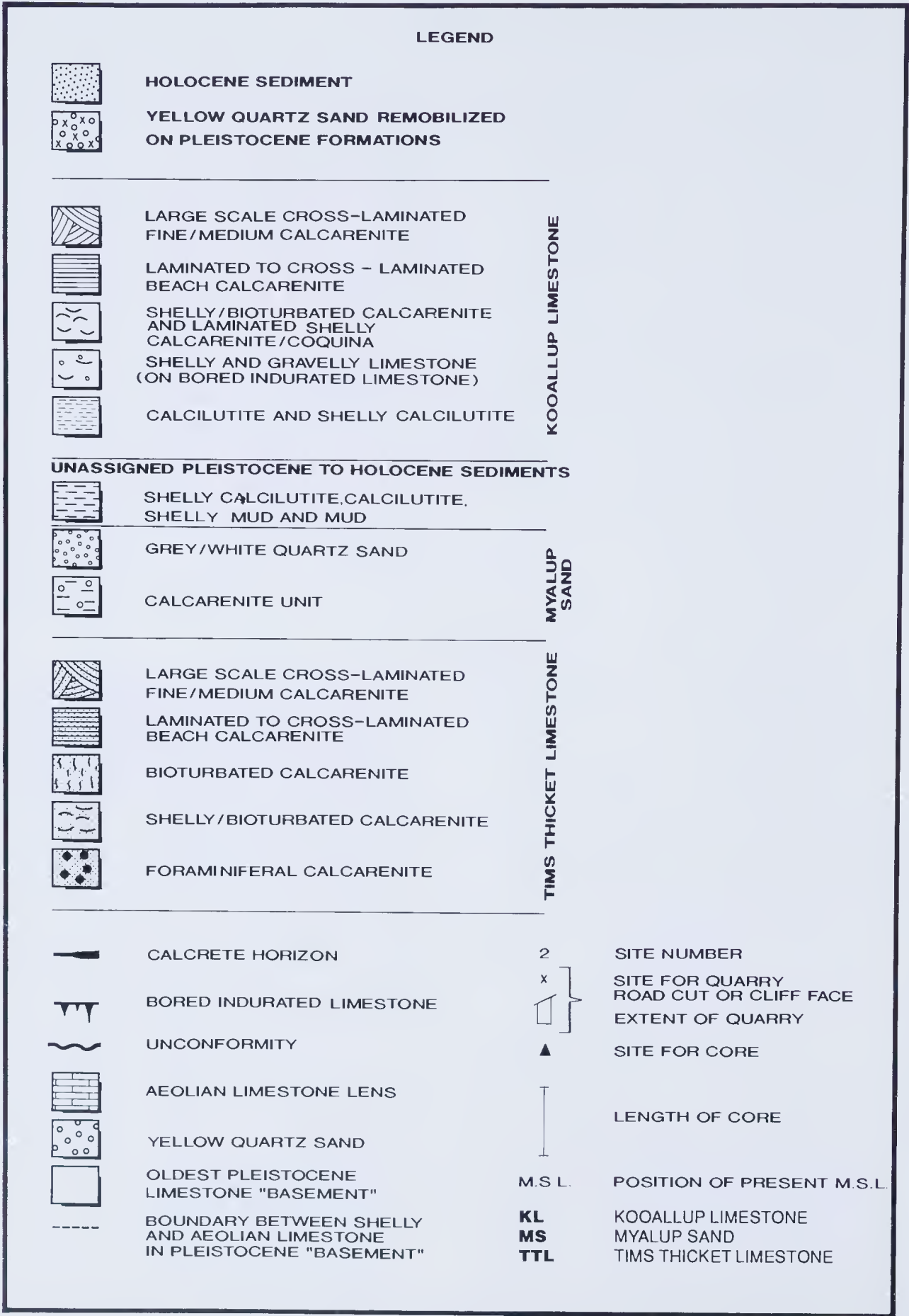


Figure 2A. Stratigraphy of transects. Legend to transects.

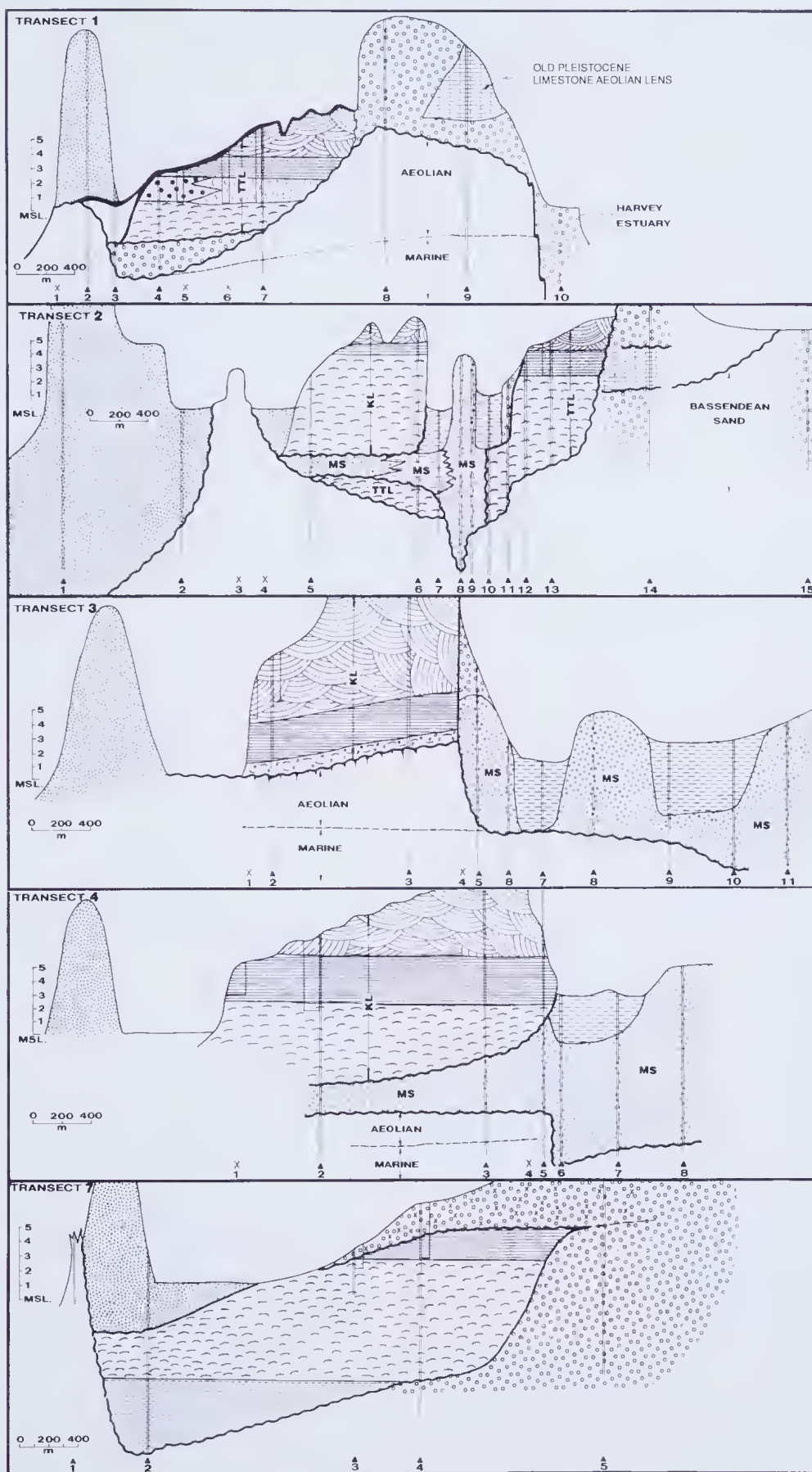


Figure 2B. The stratigraphy of the transects 1-4, 7.

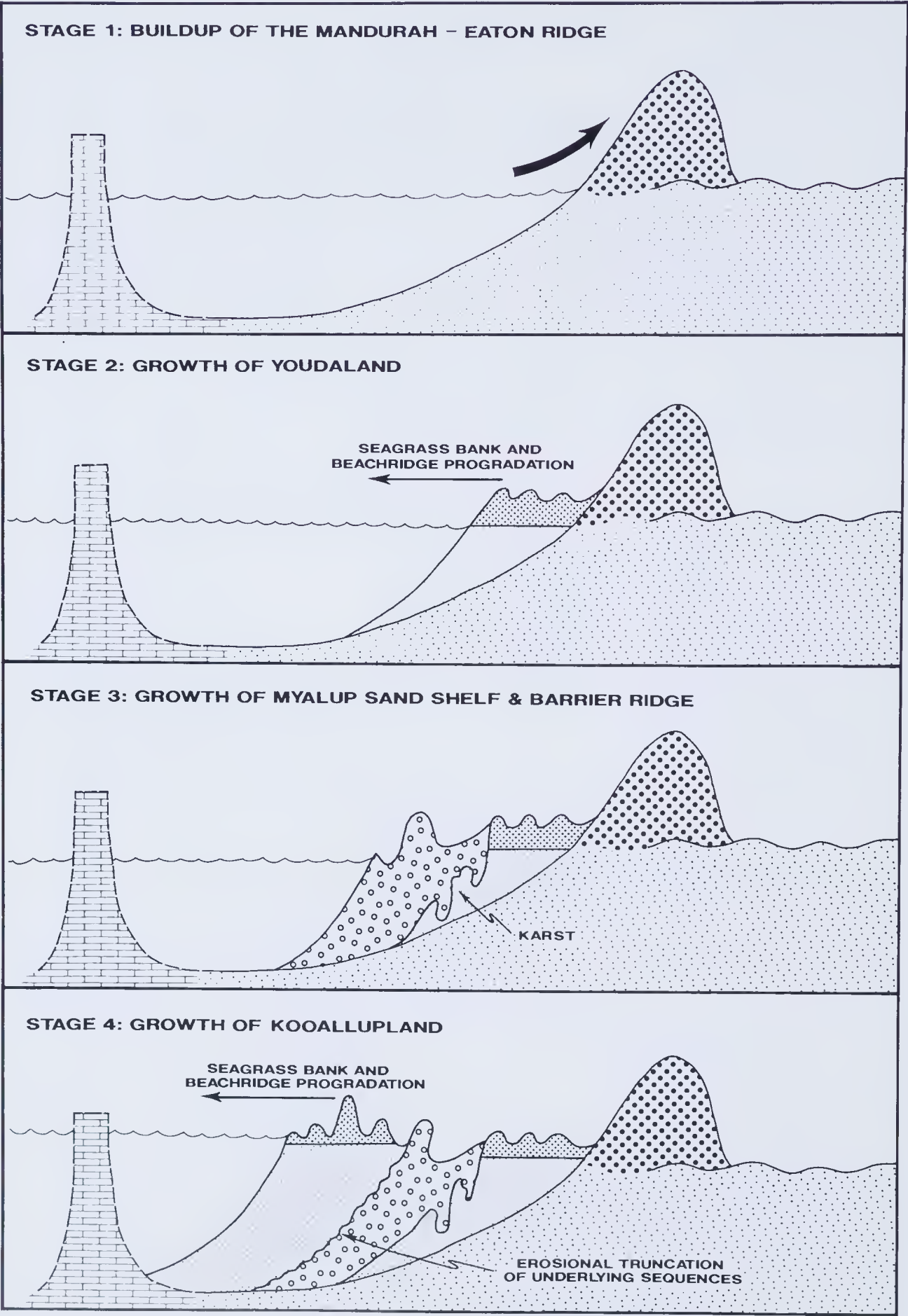


Figure 3. Summary of stratigraphic relationships between the Pleistocene formations (from Semeniuk 1995a).

2. bioturbated foraminiferal calcarenite: 1.8 m thick;
1. shelly/bioturbated calcarenite with seagrass assemblage biota: 2.0 m thick; unconformable on yellow quartz sand.

The bioturbated foraminiferal calcarenite is laterally equivalent to shelly/bioturbated calcarenite and laminated and cross-laminated marine calcarenite. The limestone types in the formation are in a shoaling-upward sequence, with seagrass bank lithofacies and the laterally equivalent sand wave lithofacies and bioturbated foraminiferal calcarenite lithofacies passing up into a beach sequence and then into a beachridge/dune sequence. Within the beach facies, the subfacies are also in a shoaling sequence: trough cross-bedded calcarenite passes up into laminated calcarenite with *Donax* (a beach zone indicator), into calcarenite with bubble structures, into structureless calcarenite with *Sepia* and *Spirula*, and then finally into large scale cross-laminated aeolian calcarenite.

Stratigraphic relationships: The formation unconformably overlies older Pleistocene limestone at depth, abutting and pinching out unconformably to east against yellow sand and limestone that underlie the Mandurah-Eaton Ridge, and pinches out downdip (westwards) as a natural palaeogeographic synoptic surface. In its eastern parts, it is unconformably overlain by the Myalup Sand filling karst features on the limestone; in its western parts it is unconformably overlain by Holocene sediment.

Fossils: Lower to middle parts of the formation contain molluscan and foraminiferan fossils, indicative of seagrass bank environments. The molluscs are listed and compared with the Holocene seagrass bank assemblage in Table 1. The upper part of the unit, the beach facies, contains *Donax* spp, *Paphies* sp, *Sepia* spp, and *Spirula spirula*.

Members in the formation: The natural lithologic sequence in the formation reflects a sequence of shoaling, with seagrass bank lithofacies and the laterally equivalent sand wave lithofacies and bioturbated foraminiferal calcarenite lithofacies passing up into a beach sequence and then into a beachridge/dune sequence. In a broad view, the formation consists of a distinctive mid-lower part of fossiliferous limestones passing up into aeolian limestones. It is proposed that the broad separation of the calcarenites from fossiliferous submarine to littoral to non-fossiliferous aeolian be the basis of recognising two members in the formation, as follows (Table 2):

White Hill Road Limestone Member: upper part of formation consisting of aeolian calcarenite. The area along White Hill Road, south of Mandurah, exposes good sequences of this member, with relict beachridge patterns evident (see figure 5 of Semeniuk 1995a). The type location for the member is the same as for the formation.

Clifton Downs Member: lower to middle part of the formation consisting of fossiliferous marine calcarenite passing up into fossiliferous laminated beach calcarenite, exposed in the Clifton Downs area, east of Lake Clifton. The type location for the member is the same as for the formation. Additional quarry reference sites are located along Tims Thicket Road in the Tims Thicket area.

Myalup Sand

Definition and characteristics: The Myalup Sand is a predominantly grey to white quartz sand unit between the Tims Thicket Limestone (below) and the Kooallup Limestone (above). There are local thin lenses of limestone in the formation.

Derivation of name: Myalup Swamp, in the southern Yalgorup Plain area, east of Binningup.

Type section: Sand ridge at 32°58'00" 115°42'57", south of the Yalgorup National Park.

Distribution: The formation is restricted to the Yalgorup Plain, cropping out almost along the entire length of its eastern and middle part. It also is intersected in core in this area.

Thickness and geometry: Where intersected in core and trenches, the formation has variable thickness from 5–15 m thick. Regionally, the unit is a ribbon to shoestring, some 60 km long, up to 5 km wide and 5–15 m thick.

Lithology: The type section, 15 m thick, is generally structureless grey to white quartz sand, mainly fine to medium sand-sized, and poorly sorted. The formation becomes progressively more iron-stained in the upper 3–4 m. Though quartz rich, it also contains minor feldspar. The upper parts of the formation may be stained yellow. Locally, there are carbonate-rich lenses, <1 m thick, located 2–3 m below present mean sea level. It was not generally possible to differentiate facies in the quartz sand sections of the Myalup Sand.

Stratigraphic relationships: Contact with the underlying Tims Thicket Limestone is sharp and unconformable, marked by prominent karst in the limestone. Contact with the overlying Kooallup Limestone is sharp and unconformable, with the base of the limestone truncating the ridge-and-depression sequence in the Myalup Sand which pinches out under the limestone. In the depressions on the Myalup Sand, there is an overlying undifferentiated suite of Pleistocene to Holocene shelly terrigenous mud, calcilutite and shelly calcilutite (wetland and estuarine facies). The contact of Myalup Sand with the sediments that underlie the Mandurah-Eaton Ridge is difficult to differentiate.

Fossils: No fossils has been retrieved from the formation, but the limestone lenses therein hold scope to be fossiliferous.

Kooallup Limestone

Definition and characteristics: The Kooallup Limestone is a Pleistocene fossiliferous and non-fossiliferous calcarenite that crops out along the western zone of the Yalgorup Plain. Subsurface sections may contain local calcilutite lenses. The lower to middle part of the formation is fossiliferous, and the uppermost part is aeolian.

Derivation of name: Kooallup Lagoon, east of Lake Preston and north of Myalup.

Type section (type locality): Quarry, east of Lake Preston, in the southern part of Yalgorup Plain area, at 32°02'46" 115°42'36".

Distribution: The formation is restricted to the Yalgorup Plain area, cropping out almost along the entire length of the western part of the Yalgorup Plain. Additionally,

it has been intersected in core underlying Holocene units in this region.

Thickness and geometry: At the type section, the formation is 10.8 m thick. Regionally, the unit is a ribbon to wedge, some 60 km long, up to 5 km wide and 5–16 m thick.

Lithology: At the type section, there are four types of limestone; in stratigraphic order, from 1 at the base to 3 at the top, these are:

3. cross-laminated to structureless calcarenitic aeolianite: 1.8 m thick;
2. laminated to cross laminated beach calcarenite: 3.0 m thick;
1. laminated and cross laminated marine calcarenite and shelly/bioturbated calcarenite with seagrass assemblage biota: 6 m.

In a section further south from the type section, the same sequence of limestones occur but are underlain by calcilutite:

3. laminated to cross laminated beach calcarenite: 2 m thick;
2. laminated and cross laminated marine calcarenite: 9 m thick;
1. shelly calcilutite (5 m thick); unconformable on an older un-named shelly marine limestone.

In general, the Kooallup Limestone sequences exhibit shoaling: seagrass bank facies, and the laterally equivalent sand wave facies, are overlain by beach and then beachridge/dune facies. The beach sequence progresses from subtidal to supratidal, with preservation of bubble structures and shells of *Donax*, *Sepia*, and *Spirula*. Locally, in former inter-ridge marine depressions, there are lenses of calcilutite.

Stratigraphic relationships: The formation unconformably overlies an older as yet un-named Pleistocene limestone at depth, and pinches out unconformably to the east against the Myalup Sand. To the west, it pinches out downdip as a natural palaeogeographic surface, or abuts a buried ridge that is the extension of the Bouvard Reefs system.

Fossils: The fossil within the Kooallup Limestone is similar to that in the Tims Thicket Limestone. The lower to middle parts of this formation contain molluscs (Table 1) and foraminifera, derived from seagrass bank environments. The upper part of the unit, the beach facies, contains *Donax* spp, *Paphies* sp, *Sepia* spp, and *Spirula spirula*.

Members in the formation: As for the Tims Thicket Limestone, the sequence in the Kooallup Limestone reflects shoaling, with (local basin calcilutites and) seagrass bank lithofacies passing up into beach facies and then into a beachridge/ dune facies. The sequences essentially form a fossiliferous lower to middle part, and a non-fossiliferous (aeolian) upper part. It is proposed that this broad separation of limestones be the basis of recognising three members in the formation, as follows (Table 2):

Lakeside Limestone Member: upper part of formation consisting of aeolian calcarenite. The type location for the member is the same as for the formation; additionally, the pits and quarries around the Lakeside property east of Lake Preston, and

the eastern shore of Lake Preston exposes good sequences of this member.

Bellevue Limestone Member: lower to middle part of formation consisting of fossiliferous marine limestones and fossiliferous laminated beach calcarenite. The type location for the member is the same as for the formation; additionally, local pits and quarries in the area of the Bellevue property, along the northeastern shore of Leschenault Inlet, expose good sections of this member.

Springhill Limestone Member: lower part of the formation consisting of calcilutite and shelly calcilutite. A local lens of this calcilutite occurs at depth under the Springhill property (located 2 km SE of Binningup). The type section for the member is Core Site 2, Transect 7 (Fig 2). [Note that use of the Springhill Limestone Member is to be distinguished from the previous use of the term Spring Hill, as two words, for the Palaeozoic Spring Hill Limestone in the Bonaparte Basin; though not formally defined to date in the Bonaparte Basin, the Spring Hill Limestone was first used by Druce 1963].

Distribution: An additional feature in the Kooallup Limestone is a south to north facies change; to the south, beachridge and dune facies above the seagrass bank and beach facies are quartz sand rich; to the north, they are more carbonate-grain rich. This transition is related to major inputs of quartz sand from two sources in the south: erosion of the Mandurah-Eaton ridge (with concomitant net northwards longshore drift), and the Colly, Preston and Wellesley rivers transporting quartz from the dunes further east.

Pleistocene palaeogeographic units

The Pleistocene formations are restricted to distinct, mappable tracts of country that represent discrete phases of coastal sedimentation, progradation, and geomorphic history in this region. In effect, their distribution reflects accretionary stages of the Swan Coastal Plain between Mandurah and Bunbury. In this context, they have been assigned palaeogeographic names to highlight their discrete palaeogeographic character (Semeniuk 1995a). The distribution of the Pleistocene formations in relationship to the Pleistocene landform units are as follows (Semeniuk 1995a):

1. **Youdaland:** the most eastern and oldest Pleistocene landform unit on the Yalgorup Plain, underlain by the Tims Thicket Limestone; the name derives from Youda, between Tims Thicket and Mandurah;
2. **Myalup Sand Shelf and Myalup Sand Ridge:** a sand shelf system that separates the Mandurah-Eaton Ridge from Kooallupland, and a linear ridge system generally sandwiched between the Youdaland and Kooallupland, respectively, and underlain by the Myalup Sand; the name derives from Myalup Swamp, between Myalup and Binningup; and
3. **Kooallupland:** the most western and youngest Pleistocene landform unit on the Yalgorup Plain, underlain by Kooallup Limestone; the name derives from Kooallup Lagoon, located to the east of Lake Preston.

The evolution of the Yalgorup (coastal) Plain is interpreted to have taken place in several stages related to sealevel still-stands in the Pleistocene (Semeniuk 1995a):

1. formation of an older Pleistocene limestone beachridge plain (Youdaland), within which there was shoaling from

marine seagrass carbonate sedimentation to beach to beachridges/dunes;

2. accumulation of quartz rich coastal sand barriers (Myalup Sand Shelf and Myalup Sand Ridge);

3. formation of a younger Pleistocene limestone beachridge plain (Kooallupland) within which there was, again, shoaling from marine seagrass carbonate sedimentation to beach to beachridges/dunes.

Thus the overall progressive accretion of the Yalgorup Plain records, with subaerial interruptions (Fig 3); 1, sedimentation and progradation in a coastal setting partly behind offshore rocky reefs; 2, changes in style from cusate foreland and shoreface accretion to coastal barriers; and 3, alternation in sedimentation from carbonate-rich to quartz-rich. The results also provide several insights into the Quaternary history of the Perth Basin in southwestern Australia in regards to the alternations of carbonate/siliciclastic sedimentation in general, the control of the geometry of coastal sediment bodies by ancestral topography such as the offshore limestone ridges, the longevity of the limestone ridge ancestral topography, and the age structure of the Pleistocene coastal plains (Semeniuk 1995a).

Holocene stratigraphy

Much of the western edge of the Yalgorup Plain is bordered by Holocene barrier dunes. Though these are a geomorphic extension of the Leschenault Peninsula barrier (Semeniuk 1985), stratigraphically they present a different Holocene history to elsewhere. Various Holocene sediment types occur in this area and, generally, they can be assigned to previously defined formations. However, one unit remains undescribed, and is formally defined in this paper as the Preston Beach Coquina. The sediment types and their assigned formations are summarised in Table 3.

Preston Beach Coquina

Definition and characteristics: The Preston Beach Coquina is the name proposed for light-coloured, bedded, laminated, cross-laminated shell gravel and shelly sand along the shoreface of the Leschenault-Preston Sector, and in the subsurface.

Derivation of name: Preston Beach, south of Mandurah.

Type section: Preston Beach at 32°52'57" 115°38'40".

Distribution: The unit is widespread along the coastal zone of the Leschenault-Preston Sector, and additionally forms isolated units in the subsurface in other coastal sectors further north.

Thickness and geometry: The unit is up to 6–7 m thick. Regionally along the Leschenault-Preston Sector, the unit will appear as a discontinuous ribbon, some tens of kilometres long, up to 100–200 m wide and 6–7 m thick. Elsewhere it forms lenses, some 1–3 m thick, and hundreds of metres wide.

Lithology: At the type section, the formation is a light-coloured (yellowish, tan, buff, to cream), bedded, crudely layered, to locally laminated, to cross-laminated deposit of shell gravel, shell grit, shelly sand, and sand. Sand grains are quartz, or quartz, bioclasts and lime-

stone lithoclasts. The upper 1 m of the unit also has a distinctive deposit of storm debris, with *Sepia* spp and *Spirula spirula*, mixed shell, and local horizons of pebbles of pumice.

Stratigraphic relationships: The formation overlies a variety of units, depending on locality and the extent of erosion along its base: it has an erosional contact with both the Becher Sand and Leschenault Formation, and an unconformable contact with Pleistocene sediment and sedimentary rock. The formation is overlain conformably and gradationally by dune deposits of the Safety Bay Sand. Laterally, the unit may pass into shelly sand and sand of the beach facies of the Safety Bay Sand. It may also pass laterally into Becher Sand.

Fossils: Molluscan shell remains in the formation include: *Donax* spp, *Glycymeris* sp, *Macra* sp, and *Donacilla* sp, and in the uppermost part, *Spirula spirula* and *Sepia* spp.

Age: Radiocarbon ages show that the unit is wholly Holocene. In the Leschenault-Preston Sector, its age is 5455 ¹⁴C yrs BP to present (Semeniuk 1995b). Elsewhere, such as at Quinns Rock, it is older, but still Holocene.

Distribution: The Preston Beach Coquina is a distinctive, widespread shell gravel unit formed in high energy beach to shoreface settings. The dominant, and consistent shell gravel content serves to separate it from other marine and strand units such as the Becher Sand and the beach facies of the Safety Bay Sand, respectively.

Holocene sedimentary sequences

In coastal southwestern Australia, there are four main large-scale standard Holocene stratigraphic sequences (Semeniuk 1995b, and Fig 4):

Type 1, prograded bank, beach, beachridge system composed of a shoaling sequence of subtidal basin sediment, seagrass bank sediment, beach sand, and dune sand;

Type 2, prograded shoreface to beachridge system composed of a shoaling sequence of shoreface shell/sand, beach sand/shell, and dune sand;

Type 3, retrograded barrier dune system composed of dune sand overlying estuarine lagoonal sediment; and

Type 4, retrograded barrier dune system composed of dune sand unconformable on Pleistocene sediment.

Each type tends to be localised in a specific sector of coast. Type 1 occurs in settings of cusate forelands behind barrier limestone reefs, ridges and islands, such as the Rockingham-Becher system (Searle *et al.* 1988) and the Whitfords Cusp (Semeniuk & Searle 1986). Type 2 occurs along the modern shore face of the Leschenault-Preston barrier (*e.g.* Preston Beach). Type 3 occurs in the Leschenault Peninsula area (Semeniuk 1985), and Type 4 occurs in the northern part of the Leschenault-Preston Sector and in coastal sectors further north (Semeniuk *et al.* 1989).

Barrier dune stratigraphy, Yalgorup area

The standard Holocene stratigraphic sequences have been used to help unravel the Holocene history of the barrier dunes in the Yalgorup area, and specifically between Preston Beach and the Bouvard Reefs. The Holocene stratigraphy under the barrier dunes here is complex;

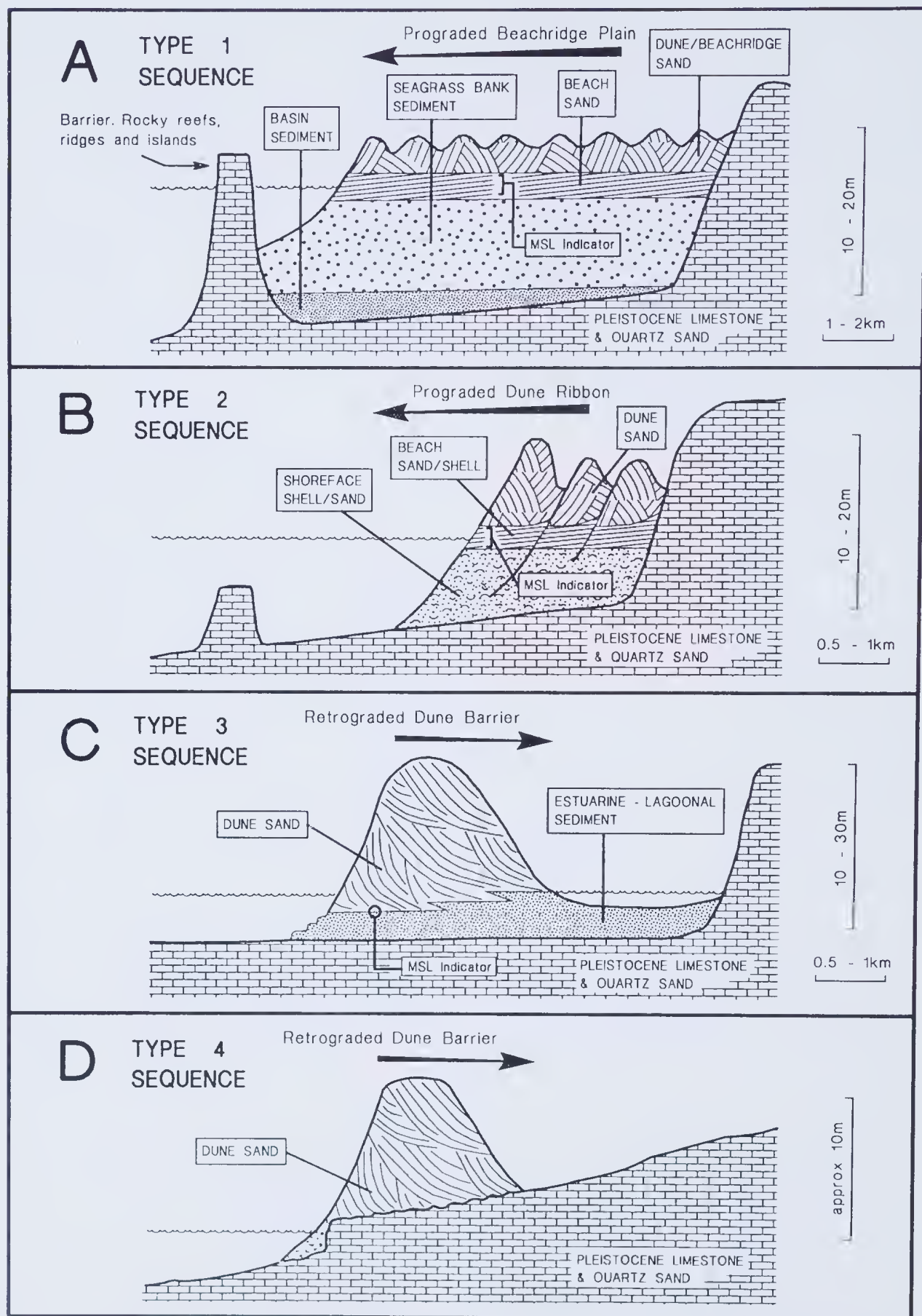


Figure 4. The four standard Holocene stratigraphic sequences in the southern Perth Basin (from Semeniuk 1995b).

the marine Holocene record begins with a Type 1 sequence, which is sharply overlain by a Type 3 sequence, with a final capping of Type 2 sequence (Semeniuk 1995b). The sedimentary sequence records dramatic coastal changes associated with rising Holocene sealevels; simple seagrass bank, beach, beachridge sedimentation/progradation was abruptly terminated, and succeeded by development of a barrier dune with its associated barred lagoon. The sequence developed is interpreted to be a response to seas rising into a bathymetrically complex area. The area between Preston Beach and Bouvard Reefs, being in a transition zone between a coastal sector of complex bathymetry to the north and one of simple bathymetry to the south, had the potential to record differing styles of Holocene sedimentation in response to varying sealevel (Semeniuk 1995b).

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Seagrass communities in Exmouth Gulf, Western Australia: A preliminary survey

L J McCook, D W Klumpp & A D McKinnon

Australian Institute of Marine Science, Cape Ferguson, PMB 3, Townsville MC QLD 4810

Manuscript received July 1995; accepted October 1995

Abstract

A preliminary survey of seagrass communities in Exmouth Gulf, Western Australia, found very low abundances of seagrasses. This seems surprising given the abundance of seagrass beds elsewhere in northern and western Australia, and the highly productive prawn fishery in the gulf; prawn fisheries are usually associated with seagrass systems. Quantitative and qualitative survey of 64 sites, mainly in the inaccessible south and east of the gulf, in September 1994, indicated that seagrasses were neither extensive nor abundant. Percent covers were rarely over 5-10%. Predominant seagrasses were species of *Cymodocea* König, at depths of 0-5 m, and *Halodule* Endlicher in intertidal areas. Species recorded were largely in accordance with published distribution ranges. Subjective assessments indicate that epiphytic and epilithic ephemeral macroalgae contribute significant amounts of production, compared to seagrasses. The lack of extensive seagrass beds is considered in terms of the physical environment of the gulf, and in terms of the carbon source for the highly productive prawn fishery. Despite the ecological and economic importance of seagrasses, this survey is only the second published account of seagrasses for the coast between Shark Bay, Western Australia, and the Gulf of Carpentaria.

Introduction

Seagrass beds are of major ecological and economic importance to coastal ecosystems, particularly in tropical Australia (e.g. Larkum *et al.* 1989; Poiner *et al.* 1989; Pollard *et al.* 1993); yet very little is known about seagrasses throughout the north-west of Australia. There has only been one published survey (Walker & Prince 1987) of seagrass communities between the Gulf of Carpentaria and Shark Bay (Western Australia), roughly a quarter of Australia's coastline.

In north-east and western Australia, seagrass beds are important in terms of area (Kirkman & Walker 1989; Lee Long *et al.* 1993; Coles *et al.* 1989) and primary production/standing crop (Walker *et al.* 1988; Walker 1989; more generally Klumpp *et al.* 1989; Hillman *et al.* 1989), and as nursery habitats for commercial and recreational fisheries. Seagrass beds in Shark Bay, about 450 km south of Exmouth, are amongst the most extensive, productive and diverse described, with very high standing crops (Walker *et al.* 1988; Walker 1989; Kendrick *et al.* 1990). In the Gulf of Carpentaria, Torres Strait and Great Barrier Reef regions, considerable work has emphasized the extent of seagrass beds and their importance as prawn and fish nurseries (Coles *et al.* 1987, 1989, 1993a,b; Poiner *et al.* 1989; Lee Long *et al.* 1993).

In north-west Australia, Walker & Prince (1987; also Prince 1986, *pers. comm.*) qualitatively surveyed seagrass species distributions at a wide range of locations. Seagrass diversity was found to be high, with an overlap of southern temperate and tropical Indo-Pacific species. These distributions were critical to interpretations of a centre of seagrass diversity and speciation in New

Guinea (Walker & Prince 1987; Kirkman & Walker 1989). More detailed surveys of some north-west shelf marine habitats have been carried out for the oil and gas industries, as far south as Exmouth Gulf, but this information is proprietary (R Hilliard, LeProvost, Dames & Moore Ltd, *pers. comm.*). Poiner *et al.* (1989) identified an urgent need for information on north-west Australian seagrasses.

The present study describes seagrass community composition in Exmouth Gulf, north-west Australia, with an emphasis on the relatively inaccessible and shallow east coast. Exmouth Gulf is a large shallow basin set in a remote, arid tropical area (22°S), enclosed by the Cape Range on the west, and by extremely arid plains to the east (Fig 1). The west coast is largely sand beaches and most of the east coast has a narrow fringe of mangroves bordering extensive salt flats (up to 10 km wide). Rainfall and river runoff in the area are extremely low, and depend on rare floods resulting from cyclones. There is very little published information on marine habitats in Exmouth Gulf, despite its area ($\approx 3,000 \text{ km}^2$) and the presence of a highly productive prawn fishery ($> 1,000$ tonnes *p.a.*, R Watson, Fisheries Department of WA 1991 and *pers. comm.*) and several oil exploration projects in the area (WA Environmental Protection Agency 1991a, b). There is very little information on the east coast of the Gulf, which is inaccessible by road (Start & McKenzie 1992).

Methods

The survey, which took place between 24 and 30 September 1994, focused on five areas approximately regularly spaced on the eastern and southern coasts of the Exmouth Gulf, and one area on the west coast (Fig 1).

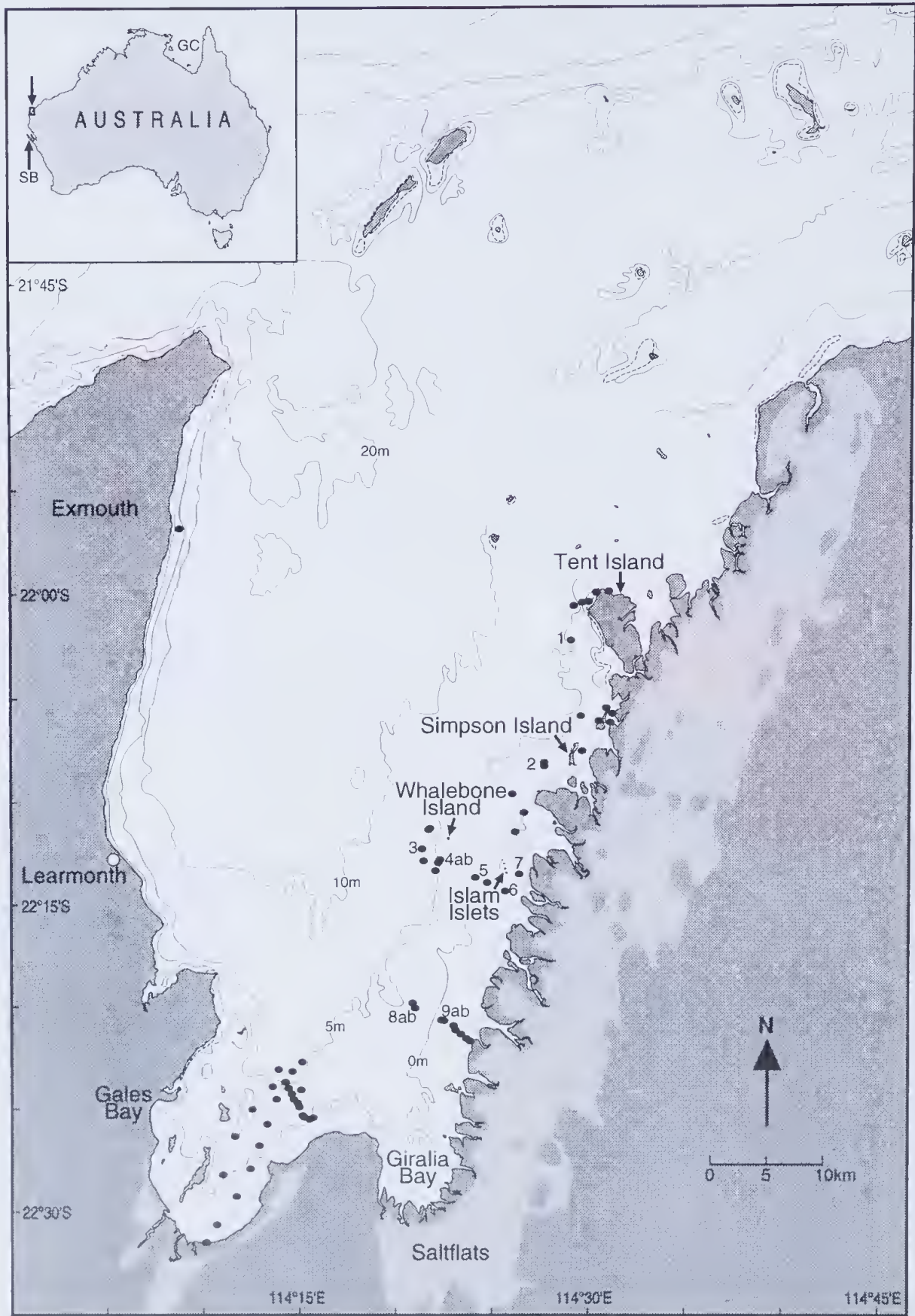


Figure 1. Map of Exmouth Gulf, Western Australia, showing survey sites (●). Numbers indicate sites for quantitative estimates of community composition made on 50 m transects. On the inset, SB and GC indicate Shark Bay and the Gulf of Carpentaria, respectively.

We combined qualitative observations, intended to describe type and extent of benthic vegetation, with systematic quantitative sampling in areas where seagrasses were most abundant. This approach was an adaptation of planned systematic sampling in response to low abundances. Where seagrasses were absent or extremely sparse, quantitative data were not collected. Qualitative spot checks also indicated the representivity of the quantitative data. The west coast site was immediately opposite Norcape Lodge, Exmouth township. The survey focused on the extensive shallow and tidal areas of the southern and eastern gulf, which have little or no road access. Lack of time and navigation information restricted the survey to south of Tent Island.

The quantitative sampling involved estimating abundance of biota at 5 replicate, randomly placed quadrats on a 50 m transect haphazardly laid in areas where spot checks indicated seagrasses to be present in measurable amounts. At each point, we estimated: (i) % cover of seagrasses (by genera, or species where easily distinguished *in situ*) and algae (in functional groups) using 100 points on a 1 m² string grid; and (ii) density of seagrasses and any abundant macro-invertebrates using a (50 cm)² quadrat (density estimates at site 7, a *Halodule uninervis* bed, used a (25 cm)² quadrat, with data scaled accordingly). Density was counted as numbers of erect shoots (leaf groups/clusters) per quadrat. At three sites (4, 8 & 9), we did two transects separated by about 1-200 metres, to indicate variability in abundance (patchiness) at that scale. At sites 2-6, we also collected all plant matter in (50 cm)² quadrats for biomass estimates. This material was frozen and later thawed, blotted, separated into above ground and below ground fractions, and wet weighed. Qualitative surveys involved spot checks of benthic community composition, water depth and substrate composition. Where seagrass fronds were not seen, their absence was confirmed by checking for rhizomes in the sediment. Depths were estimated from diving depth gauges and corrected relative to tidal datum by interpolation. Latitude and longitude were determined using a hand-held GPS (Global Positioning System, Motorola Trx 61000A5). Salinity (portable salinometer) and turbidity (secchi disk) were measured as part of another study (McKinnon & Ayukai *in press*). Since this survey focussed on seagrasses, detailed information on algae was not collected. Seagrass specimens were pressed and lodged with the Herbarium of the University of Western Australia.

Results

Seagrasses were neither extensive nor abundant throughout the areas surveyed. Seagrasses were rare or absent below 5 m (below datum), and even in areas with the greatest abundances, percent cover was rarely over 5% (Fig 2). Extensive areas of shallower water, especially in the southern Gulf (Gales Bay & inshore of site 9, Fig 1) had little or no vegetation, but bare sandy or gravelly substrate, often with a fine film of cyanobacteria. In the shallow mid-east of the gulf, sparse beds of *Cymodocea serrulata* (R. Br.) Aschers. and Magnus and *Cymodocea angustata* Ostenfeld were common between low tide level and 5 m, but these were generally very low in biomass and often patchy. Leaf blade lengths

were generally about 5 cm and always less than 10 cm. We found two dense beds of *Halodule uninervis* (Forsk.) Aschers. in Boissier in shallow intertidal areas near Islam Islets (site 7) and Simpson Islet (east of Burnside Islet) and a small bed of *Syringodium isoetifolium* (Aschers.) Dandy also near Burnside Islet. However, these were limited in extent, relative to the area of apparently similar habitat. Specific searches for roots or rhizomes in the sediments never indicated greater abundances than indicated by above ground shoots.

Quantitative data on community composition (Fig 2) show that even the areas with most abundant *Cymodocea* beds were rarely over 5% cover (maximum cover measured was 6%, but higher cover was noted at the north end of Tent Island). Small amounts of *Halophila ovalis* (R. Br.) Hook F, *Halophila spinulosa* (density ≤ 16 m⁻²), *Syringodium isoetifolium* (R. Br.) Aschers. (density ≤ 144 m⁻²) and occasionally *Halodule* were present in *Cymodocea* beds, as were species of the algal genera *Caulerpa*, *Halimeda*, *Udotea*, and *Penicillus*, all Chlorophyta.

Halodule beds had a higher % cover than *Cymodocea* beds, as well as a high % cover of fairly fine ephemeral algae (Fig 2). However, the mean cover (site 7) was only 21% and these beds were apparently quite limited in extent.

Importantly, there were often large quantities of algae, attached to and/or entangled with the seagrass or attached to shells or subsurface rock. These algae included a wide range of groups, from fine filamentous turfs, through ephemeral epiphytes such as *Hydroclathrus*, *Padina*, *Sporocninus*, *Dictyota*, *Asparagopsis*, *Laurencia*, *Dictyomenia tridens*, *Gracilaria* and *Hypnea* to perennial macrophytes, notably *Sargassum decurrens* (R Brown ex Turner) C Agardh and *Sargassum* spp. The ephemeral phaeophyte *Hydroclathrus* was particularly abundant. In some transects, the cover and biomass of these algae was greater than that of the seagrasses, despite the selection of sites on seagrass beds (Fig 2). Indeed, there were extensive, shallow subtidal areas with thick beds of these ephemeral and perennial algae, attached either epiphytically on very sparse seagrass rhizomes, or on hard substrate. Of the areas surveyed, algal beds were most abundant from Tent Island to Whalebone Island/Islam Islets. Large amounts of these species were common throughout the Gulf, both as unattached surface drift, and on the bottom as drift still attached to small fragments of shell etc.

Benthic invertebrates were apparently generally sparse, although we did not sample in detail for burrowing species. Bivalves, starfish, holothurians, small gastropods, decapods and hermit crabs were observed, as well as many small corals, particularly mussels. In one area (site 1, depth 5 m) we found abundant cockles (*Anadara scapha* mean density 38.2 per 0.25 m², standard deviation 7.95), but these cockle beds were not found further south. Amphipods were common on collected plants. Small gastropods and hermit crabs were observed amongst seagrasses, but were not abundant. Plant matter was often observed trailing from burrows in the sediment.

Qualitative observations indicate that the quantitative data are generally representative of areas with most abundant seagrasses. In the area from Tent Island to

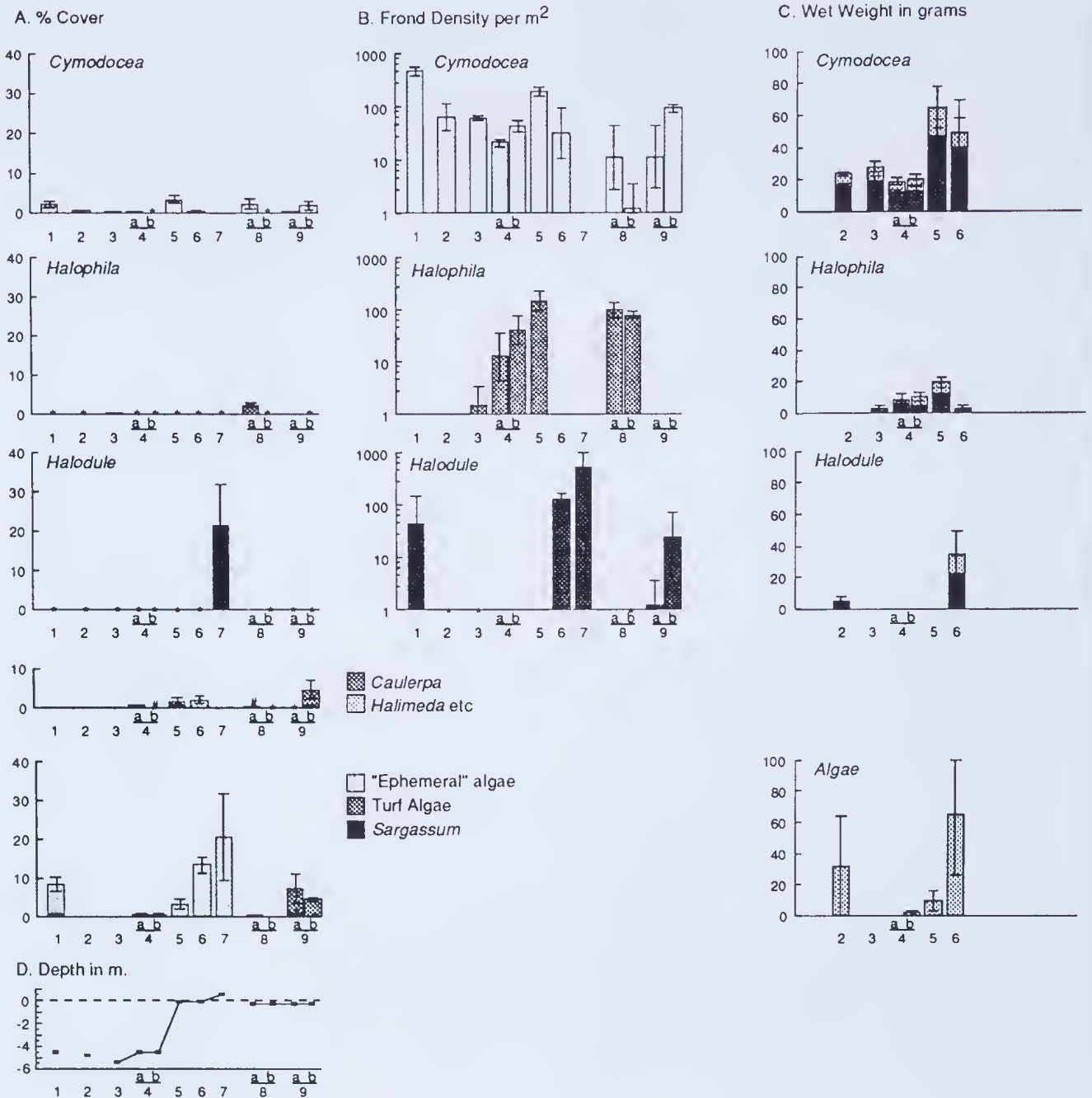


Figure 2. % Cover (A), density (B) and biomass (C) of seagrass and algal groups at a range of sites in eastern Exmouth Gulf. Depths below chart datum are shown in part (D). Site numbers (horizontal axes) refer to Fig 1. Data are mean $\pm$ se of 5 replicates. % covers of algal groups are shown as cumulative to reduce the number of graphs. "Ephemeral" algae includes non-filamentous but simple, fast growing taxa such as *Hydroclathrus*, *Padina*, *Sporochnus*, *Asparagopsis* and *Dictyota*. Densities were measured in 0.25 m² quadrats, scaled to log (density m⁻² + 0.4). *Asterisks indicate taxa present but < 1% cover or density < 1 frond m⁻². Biomass estimates are wet weights, divided into below ground (dark shading) and above ground (lighter shading) plant fractions. Wet weight error bars are se of below ground and total weights. Note that biomass estimates are only available for sites 2-6. Samples were not collected at the other sites. As discussed in the text, these data are for the areas with most abundant seagrasses, since quantitative data were not collected where seagrasses were even more sparse.

Islam Islets and Whalebone Island (Fig 1) there were extensive algal beds in the shallow subtidal zone, often attached to hard pavement. Further south, spot checks inshore of site 9 found largely bare substrate with no seagrass, although *Sargassum* was present on hard substrate. Gales Bay, in the south-west, had a largely

bare sandy substrate from 7 m to the intertidal, with occasional sponges, bivalves, tunicates, soft corals and small, filamentous algae and cyanobacteria. *Cymodocea* and *Halophila* were recorded, but in very low abundances. Large numbers of turtles were observed throughout shallow areas surveyed.

On the west coast of the Gulf, near Exmouth town beach, we swam a depth profile from 10 m to the intertidal. At 10 m, seagrasses were absent but sponges, tunicates and seaweeds, and some brown algae were present. By 8 m, brown algae (especially *Sporoclinus* sp) were abundant, as well as invertebrates and small amounts of *Cymodocea* sp, *Halophila ovalis* and *H. spinulosa*. Around 5 metres, *Halophila* species were patchy but common, particularly in sheltered positions behind coral bommies etc. In the shallow subtidal and low intertidal, there were thick beds of *Sargassum*, along with some beds of *Cymodocea* and a small patch of very thick *Thalassodendron ciliatum* (Forsk) den Hartog on rocky pavement (100% cover, but < 100 m²). Most of the intertidal zone was bare sand beach.

The shallow waters of Exmouth Gulf were very turbid, with large amounts of suspended material, due to rough sea conditions and strong tidal currents. Apart from a midday lull, the Gulf was very choppy, with chop over 1 m for much of each day, due to strong land and sea breezes. Tidal currents were strong (up to 0.7 knots). Although in deeper areas (≥ 5 m) the bottom was generally fine sand or silt and mud, in shallow areas there was often only a thin veneer of sand or gravel over hard rocky pavement. The bottom sediments appeared to be highly mobile, particularly in shallower areas, and we observed several seagrass beds with exposed rhizomes and roots, where sediments appeared to have been washed away. The highest salinity measured in the Gulf was 38.5 ‰.

Discussion

Seagrass species recorded in this survey were consistent with patterns found in a previous larger scale survey (Walker & Prince 1987, Table II; also Walker *pers. comm.* and Prince *pers. comm.*), except that our record of *C. serrulata* at Tent Island (22°S) considerably extends the southern limit of this tropical species (Walker 1991). The only other published Western Australian record is from Sunday Island, King Sound (16°S, also recorded as drift at Carnarvon 24°45'; Walker & Prince 1987). All the species recorded have tropical affinities. This is in contrast to Shark Bay where the southern temperate species *Posidonia australis* Hook f. and *Amphibolis antarctica* (Labill) Sonder & Aschers ex Ashers are common, the latter species in extensive and dense meadows (Walker 1989).

Seagrass abundance in this survey was low. Cover was generally less than 5%, mean shoot densities were always less than 1,000 m⁻² and often less than 100 m⁻², and biomass was generally less than 60-100 g wet wt m⁻². In contrast, in Shark Bay, 450 km south of Exmouth, *Posidonia australis* and *Amphibolis antarctica* are extremely abundant; *A. antarctica* reaches biomasses of 2 kg dry wt m⁻² and densities of 300-500 shoots m⁻², each being up to 2 m long (Walker *et al.* 1988), but southerly seagrasses are often more abundant (Coles *et al.* 1989). Also in Shark Bay, Walker *et al.* (1988) recorded 600 leaves m⁻² and 60-100 g dry wt m⁻² of *Halodule uninervis*, and 30% cover of *Cymodocea angustata* as understorey. Just north of Exmouth Gulf, at 21° 16' S, Walker & Prince (1987) found several hundred hectares of *C. angustata* at 30-50% cover. Maximum densities and dry weights of *Halodule*

uninervis in the Great Barrier Reef region and New Guinea are also higher than those in Exmouth Gulf (Brouns 1987; Lee Long *et al.* 1993; also Mellors *et al.* 1993). Density and biomass of *Cymodocea* in our study were within the ranges reported for the Great Barrier Reef region (Lee Long *et al.* 1993), but leaves were longer in the Great Barrier Reef region (Coles *et al.* 1987). Biomass records for *C. serrulata* in New Guinea and southern Queensland (148 and >400 g dry wt m⁻² respectively; Brouns 1987; Coles *et al.* 1989) are much higher than our values. Ratios of above and below ground biomass in Exmouth Gulf were similar to those in the literature (Brouns 1987; Moriarty & Boon 1989).

The apparent lack of extensive or abundant seagrass beds in Exmouth Gulf is surprising, given the extent of apparently suitable shallow substrate, the productivity of the gulf, and the contrast with other areas of northern and western Australia. Thus, the low abundance of seagrass recorded in our survey raises three issues: (a) the representivity of the survey; (b) the reasons for the low abundance of seagrass; and (c) the source of carbon production for the Gulf's abundant prawns, turtles and dugongs.

Our results should represent typical seagrass abundances throughout the southern and eastern Gulf. The survey is limited by the locations and particularly the time of sampling, and it remains possible that seagrasses are much more abundant in other areas, or perhaps at other times of year. However, it is very unlikely that all 64 sites fell in areas of particularly low seagrass abundance, especially given our bias to areas of relatively high abundance. Given the turbidity of the water and the clear decrease in abundance between 5 and 10 m, we presume seagrasses to be restricted to shallow areas of the Gulf. It is possible that the unsurveyed northern areas of the Gulf have more seagrass, especially given the trend to very low abundances in the southern Gulf. Lack of time and navigational information precluded survey of the north-east Gulf. Qualitative surveys over the 6 months following our study by M Forde (Bowman, Bishaw & Gorham Ltd, *pers. comm.*) largely confirmed the patterns of abundance and species composition reported here, except for seasonally abundant *Halophila spinulosa* in deeper (15 m) and less turbid water north of the Gulf.

Within the Gulf, there is no indication of higher seagrass abundances at other seasons. We found no sign of dormant or decaying rhizome/root tissues, and July-September 1994 sampling with a grapple dragged on the bottom did not indicate higher abundance or longer fronds (D Pont, M G Kailis Fisheries, *pers. comm.*). Even if seagrass leaf length were to increase at other seasons, cover would remain low without a many-fold increase in density (Fig 2) and root mass. Seasonal changes in tropical seagrasses rarely exceed two-fold changes in standing crop (Mellors *et al.* 1993 for *H. uninervis* on the Great Barrier Reef; Hillman *et al.* 1989; Lanyon *et al.* 1989) and density (Brouns 1987 for *H. uninervis* in New Guinea). In New Guinea *C. serrulata* varied seasonally by only 30% (Brouns 1987). However, just north of Exmouth, Forde (Bowman, Bishaw & Gorham Ltd, *pers. comm.*) reported large changes in *H. spinulosa* above-ground biomass over 6 months, so seasonal differences remain possible. Longer term declines in seagrass abundance may have occurred in Exmouth Gulf (e.g. Poiner

et al. 1989), but there has not been any parallel decline in prawn catches (R Watson, Fisheries Department of WA, 1991 & *pers. comm.*).

The low abundance of seagrasses in the areas surveyed probably results from the lack of suitable substrate. Much of the bottom is either hard substrate or highly mobile coarse sediments, with very little fine silt and clay, and sediments appear to be eroding rather than accumulating (K Woolfe, James Cook University of North Qld, *pers. comm.*). The seagrasses may not be able to accumulate sufficient root mass to stabilise these sediments. Neither salinity nor nutrient levels are likely to be limiting seagrasses. Salinity in the well-flushed Gulf is moderate compared to the reported tolerances (64‰ for *H. uninervis*, 50‰ for *C. angustata* (Walker 1989); 45‰ for *H. ovalis*, 75‰ for *Halodule* (Hillman *et al.* 1989). Freshwater input to the Gulf is negligible. The abundance of algae on hard substrates suggests that nutrients are not limiting, and the Gulf showed no sign of eutrophication. Trawl disturbance is not responsible for low seagrass abundance, since the areas surveyed are designated a nursery zone (D Pont, M G Kailis Fisheries, *pers. comm.*), and are largely too shallow for trawling.

Assuming that our results do represent seagrass abundance throughout the Gulf, it would seem surprising that the Gulf is a highly productive region. The yearly catch of prawns (*Penaeus latisulcatus*, *Penaeus esculentus*, *Metapenaeus endeavouri*) has been over 1,000 tonnes for 8 of the last 10 years and is not apparently declining (R Watson, Fisheries Department of WA, 1991 & *pers. comm.*). Seagrass beds are important elsewhere to prawn and other fisheries, as nursery areas (Pollard 1984; Coles *et al.* 1987, 1989, 1993a,b; Poiner *et al.* 1989; Bell & Pollard 1989; Lee Long *et al.* 1993; Watson *et al.* 1993; Hill & Wassenberg 1993; less true for *P. latisulcatus*) and probably make major trophic contributions to prawn production via detrital pathways (Klumpp *et al.* 1989). Exmouth Gulf has an estimated dugong population of 1,000 and turtles are very abundant (Prince *et al.* 1981; Prince 1986; Preen *et al.*, James Cook University of North Qld, *pers. comm.*; *pers. obs.*). Both dugongs and turtles are major seagrass grazers.

Our observations suggest that the extensive algal beds are probably major primary producers in this ecosystem. Several previous studies of dense seagrass beds have found that both macroalgae and micro-algae make important contributions to biomass and productivity (Orth & Van Montfrans 1984; Kendrick *et al.* 1990; Klumpp *et al.* 1989; Borowitzka & Lethbridge 1989; Pollard & Kogure 1993). Whilst we did not quantify their contribution, these algal beds apparently have very high turnover and export to deeper water. Most of the species observed are structurally simple, rapid growing, and fragile (especially *Hydroclathrus*). We suggest that rapid growth, high proportional breakage and losses (due to rough conditions), rapid transport by wind and tidal currents, and fast break down would make these algae major sources of detritus throughout the Gulf. Other major primary producers may include phytoplankton and salt-flat cyanobacteria. Phytoplankton production is probably not high, since standing stocks of chlorophyll *a* are low (McKinnon & Ayukai, *in press*). The extensive salt flats (5-10 km wide, Fig 1) in the high intertidal of the southern and eastern Gulf have a thick mat of

cyanobacteria which may contribute significant amounts of carbon during spring tides.

Algal, phytoplankton and salt flat production may thus contribute to the high yield of prawns, via detrital food chains (Klumpp *et al.* 1989). Algal beds may also serve as prawn nursery grounds in this area. Similarly, abundance of suitable algae could sustain large populations of green turtles, which eat both seagrass and algae. However, dugongs are believed to feed on seagrass almost exclusively (Lanyon *et al.* 1989; Erftemeijer *et al.* 1993). It is difficult to explain how an area with low seagrass abundances could apparently sustain a large dugong population. Intertidal *Halodule* beds, such as we observed, are preferred feeding grounds (Lanyon *et al.* 1989). Such beds may be more extensive than our survey indicates, or may be extensive outside our survey area. Exmouth dugongs may also consume unusual amounts of algae, since Lanyon *et al.* (1989) note that dugongs do eat algae when seagrasses are scarce. Given the vulnerable status of dugongs (IUCN 1990), the issue warrants further attention.

In summary, our results suggest that much of the extensive shallow east and south coast of Exmouth Gulf does not have abundant seagrasses, perhaps because of a paucity of suitable substrate. This raises questions about primary production in a region with high prawn production and herbivore populations. We suggest that beds of ephemeral and perennial algae may be important primary producers in the region.

Acknowledgements: We are very grateful to D Walker, H Kirkman and G Kendrick for assistance with identifications, advice, support and hospitality. We thank D Pont for preliminary data, local knowledge and advice. We greatly appreciate the cheerful field assistance of D Gaughan. We thank R Christie for technical assistance, and the skipper and crew of the AIMS research vessel RV Lady Basten. Helpful comments on the manuscript were provided by R Coles, T Done, and the reviewers. This is AIMS Publication 764.

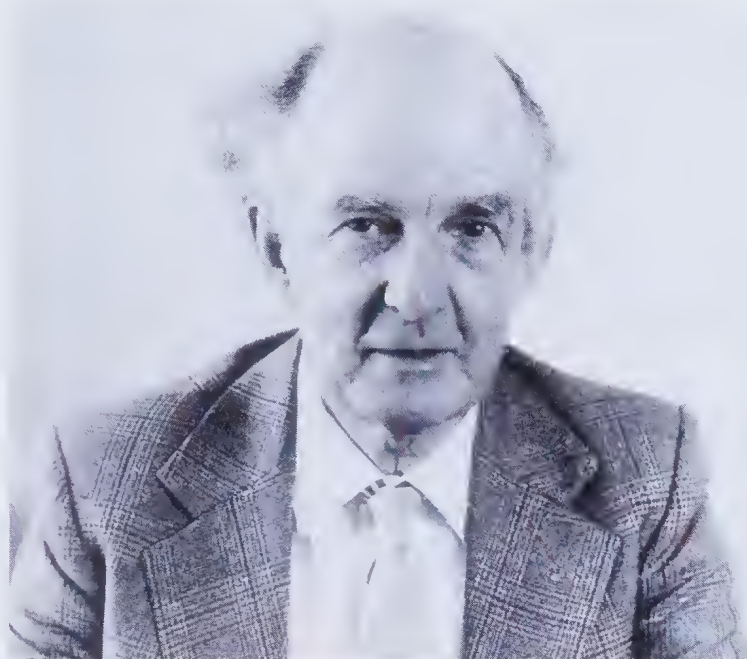
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The Royal Society of Western Australia Medallist, 1995

Emeritus Professor A R (Bert) Main



A R (Bert) Main, BSc(Hons), PhD, DSc, CBE, FAA

The Medallist for 1995, Emeritus Professor A R (Bert) Main, was elected by the Council of The Royal Society of Western Australia because of his contributions to the scientific knowledge of the natural history of Western Australia. The Medal was presented at the Royal Society of Western Australia Medal Lecture, held in the "old" Zoology Building at The University of Western Australia, by Professor Alan Robson, Deputy Vice-Chancellor of The University of Western Australia, on Monday 20 November, 1995.

Professor Albert Russell (Bert) Main was born in Perth in 1919. He grew up on a vineyard in the Swan Valley and attended Midland Junction Central School. Following a period of employment in the State Public Service, during which he studied accountancy and later towards matriculation at night school, he joined the CMF in 1939 and later AIF and saw service within Australia before joining the RAAF. After qualifying, he served as a navigator of Lancaster bombers in Europe, seeing out the last part of the war as a POW in Germany.

Upon returning to Australia he matriculated and began study at UWA financed by the Commonwealth Reconstruction Training Scheme (CRTS). He graduated in Geology and with 1st class Honours in Zoology. In 1950, he was awarded a Fulbright Scholarship to the University of Chicago. He returned from Chicago to take up an appointment in the Department of Zoology at the University of Western Australia in 1952, where he received

his Ph. D. degree in 1956. He has an Honorary Doctorate of Science from the University of Western Australia.

In 1958, Professor Main was awarded a Carnegie Travelling fellowship to the University of California at Los Angeles, in the United States of America. He was elected a fellow of the Australian Academy of Science in 1969. He received the Britannica Australia Award with Professor Harry Waring in 1970. He was elected an ANZAAS Fellow and later awarded the Mueller Medal of ANZAAS and Gold Medal of Australian Ecological Society. He was made Commander Civil Division of the Order of the British Empire CBE in 1981.

Currently, Professor Main is a member of Society for Conservation Biology; Ecological Society of Australia; Geological Society of Australia; Australian & New Zealand Association for the Advancement of Science and is an Honorary Foreign Member of the American Society of Ichthyologists & Herpetologists.

Professor Main is broadly interested in natural history, with a special interest in the ecology of animals in arid situations. He has had a long standing interest in environmental management and conservation. He served on the Fauna Advisory Committee and later the West Australian Wildlife Authority and was a foundation member and later Chairman of the Western Australian Environmental Protection Authority. He was also president of the Zoological Gardens Board. He has been a member of the Council of the Australian Institute of Marine Science in Townsville, and President of the National Parks Authority, and was a member of the Australian Universities Commission 1971-1977.

The Royal Society of Western Australia Medal Recipients 1924-1995



The Medal of The Royal Society of Western Australia was instituted in 1924 to mark the centenary of the birth of Lord Kelvin (26 June, 1825). The Royal Society Medal (originally referred to as the "Gold Medal" and then subsequently sometimes as the "Kelvin Medal" due to the association of the inaugural award with the centennial Kelvin celebration and because the medal bears in relief on its obverse side the head of Kelvin) is awarded approximately every four years for distinguished work in science connected with Western Australia.

The original dye for the medal, first struck in 1924, remains in the safe-keeping of The Society. The first three medals were struck in gold, and all subsequent medals in silver.

The first medallist of The Royal Society was Dr William J. Hancock, Government Electrical Engineer and Honorary Medical Radiographer at Perth Hospital, who in 1924 was the recipient of the Medal of The Royal Society of Western Australia, in recognition of his pioneering work in the medical application of X-rays.

The most recent medallist, Emeritus Professor A. R. (Bert) Main, was presented with the eighteenth Medal of The Royal Society of Western Australia, in recognition of his contributions to zoology.

Recipients of the Medal of The Royal Society of Western Australia are: (reference to Journal of the Royal Society notice of medal award in parentheses)

1924	Dr W J Hancock: radiography; medical application of x-rays (10:xvii)
1929	Dr E S Simpson: mineralogy and geology of Western Australia (15:iv)
1933	Mr W M Carne: plant pathology; the bitter pit of apples (19:xi)
1937	Mr A Gibb Maitland: Pilbara survey and artesian water supplies (23:xi)
1941	Prof E de C Clarke: geology of Western Australia (27:v)
1945	Mr L Glauert: natural sciences (31:vi)
1949	Mr C A Gardner: botany, the flora of Western Australia (35:v)
1955	Dr H W Bennetts: veterinary science; live stock diseases (40:1)
1959	Prof E J Underwood: animal nutrition and husbandry (43:67)
1966	Mr C F H Jenkins: agricultural entomology and natural history (49:91)
1970	Prof R T Prider: geology; petrology and mineralogy (53:95)
1979	Prof R M Berndt: anthropology; aboriginal studies (63:29)
1979	Emer Prof B J Grieve: botany; ecophysiology and the flora of WA (63:29)
1979	Dr D L Serventy: zoology; ornithology and nature conservation
1983	Dr J S Beard: botany; vegetation classification and mapping (65:93)
1986	Prof C A Parker: soil biology
1993	Prof J R de Laeter: geophysics and geochronology (77:4)
1995	Emer Prof A R Main: zoology; ecology and nature conservation (78:89)

The Royal Society of Western Australia Medallist Lecture, 1995

The study of nature – A seamless tapestry

A R Main

Department of Zoology, University of Western Australia, Nedlands WA 6907

Manuscript received December 1995

I would like to thank the Royal Society of Western Australia for their recognition of my research contributions. In a sense I am astonished that these intellectually enjoyable activities, undertaken out of my own curiosity, should be acknowledged by the award of the prestigious Royal Society Medal. I also thank Professor Alan Robson, Deputy Vice Chancellor of the University of Western Australia for personally presenting the medal. The ready and active participation of graduate students and colleagues ensured the success of all projects and I thank them sincerely.

Introduction

From time to time there have been inferences that my interests were too broad, my application undirected or that I was excessively opportunistic in my research. For example, when I was still involved with frog ecology and beginning studies of macropods, I was told by one worker that I could only expect one good idea in my life and I should stick with it. On a later occasion, another suggested that I had so many ideas that I must have stolen them. I take my cue for this lecture from these comments and briefly review and interpret the findings on the topics investigated by myself and co-workers to show that I did indeed pursue a theme of adaptations to aridity which led along many unexpected pathways.

My research has been devoted to answering questions posed by problems arising from field observations. These were initiated and conditioned by my experiences as a child when I lived within walking distance of the bush. From the time I could walk a reasonable distance, I was taken to the bush on most weekends by my grandfather and natural history mentor. I have an abiding memory of puzzlement at the contrasts between summer and winter and of wondering how so many animals managed to persist under such conditions. Briefly I was, and still am, interested in understanding the world about me. Natural History observations exposed the changes that took place but were unhelpful, except in so far as they posed testable hypotheses, in resolving the underlying mechanisms of persistence of animals or how such mechanisms may have evolved. In retrospect I now see these twin topics as motivating my curiosity about species, their adaptive traits and evolution.

It was only after war service and the benefits of the Commonwealth Reconstruction Training Scheme that I was able to gain the necessary technical skills with which to pursue my childhood interests. Parenthetically, I may comment that upon my appointment to the Zoology Department I was asked by Professor Waring what I intended to do as research. My reply embraced the points mentioned above; as soon as I mentioned evolution his comment was 'It's all known, there's nothing

to research in that'. Fortunately he did not attempt to stop me trying.

In what follows, I set out the groups of animals on which work was conducted to show the scope of the studies and to illustrate two things;

1. The interdependence of studies when interpreting observations.
2. The relevance of these studies to a wider understanding of local biology,

and how the studies led into societal issues such as conservation. I devote much space to discussing work on identification of species of frogs, the group I had chosen for comparative studies of their adaptations to aridity. But, comparative studies depend on objective identification of the species being compared, and at the start of the investigation it was not clear that systematists used objective criteria to identify Western Australian species of frogs. I present the sorting out of the problems of species' identification in some detail because it illustrates the difficulties associated with obtaining an adequate, objective, and biologically-meaningful systematic and taxonomic knowledge on which to base comparative studies of adaptation to aridity. It also explains why I have in many quarters been seen as a herpetologist rather than as an ecologist.

Frogs

Harry Waring had come to Western Australia to study marsupials, especially their reproductive physiology, and he chose to work with the quokka *Setonix brachyurus*. This species was common on Rottnest Island, and it and other marsupials that Waring and his students studied were morphologically distinct, readily identified, and posed no problems when establishing the species status of the population upon which the work was being done. This was not necessarily the case with other easily collected animals.

Prior to coming to Western Australia, Waring had worked on colour change using the South African clawed toad (*Xenopus laevis*) as an experimental animal and he was naturally favourably-inclined to frogs as experimental animals. Moreover, while there were many named species of frogs occurring around Perth, it was

not apparent that the named kinds had the same status as species that was enjoyed by marsupials. In particular, the last two workers who had reviewed Australian frog taxonomy (Loveridge 1935, and Parker 1940) held markedly different views. This was unfortunate because I had formed the view that because of the unprotected nature of their skin, frogs should be useful organisms in evolutionary studies as it was believed, at the time, that speciation in some of the biota had been promoted by a great aridity in the geologically recent past (Crocker & Wood 1947). If this were so, then adaptations to drought and their evolution might be linked to the same phenomena. But, it was necessary to first be certain that named species had a biological reality in the field and this was certainly not so as the following illustrates

In his revision of the Australian frogs of the family Leptodactylidae Parker (1940) used the flash colours in the groin to distinguish the two *Crinia* species, *georgiana* and *signifera*. These flash colours were said to be strongly developed and fast in preserved specimens of *C. georgiana* or absent or fugitive in *C. signifera*. However, when preserving specimens I had noticed that colours remained fast in either formalin or alcohol when live specimens were preserved but faded when specimens were dead before preservation. On the other hand, Loveridge (1935) believed absence of colour was indicative of *C. georgiana* whose dorsal pattern was rugose or with a few scattered warts and raised undulating glandular folds. In contrast, he classified *C. signifera* into two sub-species, *C. signifera affinis* when the back pattern was perfectly smooth without the lyre shape or *C. signifera ignita* in which a lyre-shaped dorsal fold was present. Clearly this suggested that the names assigned by museum taxonomists to species were unlikely to reflect the presence of field entities and gave no confidence that specimens agreeing with literature descriptions could be assigned names which represented biological entities which may show adaptive traits to the local environment.

Fortunately, the biological species concept had recently been proposed (Mayr 1949) and Moore's work showed the genetic inviability and hence the presence of cryptic or sibling species, within what was formerly regarded as *Rana pipiens* (Moore 1946, 1949). I already knew from observations of the many distinctive call types among local frogs that if distinct calls were assumed to reflect a specific mate identification, then putative species could be identified by collecting calling males which would represent different breeding, and hence genetically distinct, entities. The genetic distinctness of these entities could be confirmed by making crosses using Moore's technique of *in vitro* fertilisation, with appropriate controls. Normal development would be interpreted as being indicative of a within species cross, while abnormal development in the experimental cross and normal development in the control would indicate a cross between species. The sorts of abnormalities which occurred with crosses between different call types of *Crinia* were failure to develop beyond early cleavage stages, or embryos that hatched but were headless, haploid or with extruded guts. Clearly, populations used in the crosses and identified by their characteristic calls were not capable of sharing a common gene pool

and hence could not be considered as biological species in an evolutionary sense.

However, before an experimental programme could be undertaken, an objective method of recording and measuring of calls was needed. Fortunately, the Australian Broadcasting Commission co-operated by loan of equipment and running a programme on the distinctiveness of frog calls (Anon 1953). I was able to use these tapes to show by means of oscillograph analysis that different calls were distinctive in duration, repetition frequency, and pulse rate. It was now only necessary to build a portable tape recorder and the research could commence. The construction was undertaken by Murray Littlejohn, then a doctoral student, and he was able to show that a number of distinct call types could be identified in the genus *Crinia* and I was able to confirm the species status of these by means of *in vitro* crosses. At the same time Tony Lee confirmed the species status of different call types (Littlejohn & Main 1959) within the genus *Heleioporus*, which are all large burrowing frogs. A new species was also identified within the dry land burrowing frog genus *Neobatrachus*. At this stage, the conflict between Parker and Loveridge on the characters to be used in distinguishing *C. signifera* and *C. georgiana* had been resolved, the species status of *C. glauerti* had been confirmed, and sibling species of *Crinia*, *Heleioporus* and *Neobatrachus* identified (see Main 1968 for review and literature citations).

I might comment here that the recognition and naming of species using biological characteristics was not readily accepted. The substance of the objections could be reduced to two elements, species were those entities identified by recognised taxonomists, or that species should be only diagnosed by characters that were available to museum curators with access only to preserved specimens.

Once the species status of specimens could be established, it was possible to readily identify calling species in the field and so be certain of the status of collected specimens. Only then could meaningful experimental comparisons be made in the adaptive responses of the species to aridity and drought. This work was done in collaboration with Peter Bentley (Bentley *et al.* 1958; Main & Bentley 1964; Bentley & Main 1972a, b). In the midst of this work on water balance in frogs, lizards, birds and macropods, a physiologist suggested to me that it was quite improper to prostitute physiology as a field study in order to interpret the ecology of species.

The progeny arising from the controls from the *in vitro* crosses of the various call types of *Crinia* were reared to metamorphosis and these showed that the dorsal pattern so emphasised as a taxonomic character by Loveridge (1935) was an inherited trait (Main 1965).

The early work using the mating calls of males to identify species was the subject of much comment, of which the essentials were; we all know that frogs are cold-blooded vertebrates and cannot regulate their body temperature; moreover, call characteristics such as pulse rate and repetition frequency will be dependent, as in all cold-blooded animals, on body temperature; since body temperature cannot be regulated, then calls cannot be as constant and characteristic as is claimed. However, whenever calling males were collected for use in experi-

mental crosses, body temperatures were recorded and when collated these records showed specific seasons of calling and body temperature ranges for each species (Main *et al.* 1959, figs 2 and 3).

These doubts about my field-based approach produced benefits for me because Waring induced J A Moore of Columbia, then a visiting Fullbright Scholar in Australia, and later Th Dobzhansky, also of the same institution, to visit and spend time with me in the field. Waring was also instrumental in having Julian Huxley visit and accompany me in the field. I benefited immensely from these occasions and the opportunities I had to discuss evolutionary problems with them in the field. I doubt that a higher level or more intense peer review could be achieved.

I was funded in this research by University of Western Australia Research Grants, and administrators then, as now, were interested in accountability as the following illustrates. Many stores and fuel outlets in the country would not accept University purchase orders because of the perceived paper work and the delays in obtaining cash recoups. Thus I frequently had to pay cash and obtain a recoup upon my return. On one occasion, after an extensive field trip to the goldfields and pastoral areas, I was told that there were plenty of frogs around Perth and there was no need to travel, as I had done, to distant places to get them. I answered this criticism and was told not to be impertinent. When it comes to rebuking administrators who desire to limit or set boundaries of research, I hope I have not mellowed over time.

The frog work demonstrated the significance of behavioural avoidance of stressful situations as a complement to physiological adaptations. Clearly, the basis of the adaptations had been revealed and further work would involve laboratory analysis and skills which I lacked. The frog work was then reviewed and summarised by me (Main 1968).

Other Species (Reptiles and Birds)

Field work with frogs and macropods is primarily a nocturnal activity, and during the days I took every opportunity to measure the body temperatures of lizards caught in the field. During the 1960's W R Dawson, accompanied by P Licht and V Shoemaker, spent a year in Western Australia studying the temperature tolerances and biology of lizards. The data which I had already collected was assembled, and added to by them, to reveal that each species exhibited an activity pattern related to a specific temperature range (Licht *et al.* 1966).

Prior to this S D Bradshaw had begun a comparative study on *Amphibolurus ornatus* (*Ctenophorus ornatus*) which showed how intricate relationships between diet, water metabolism, electrolyte balance and behaviour led to individual survival and population persistence (Bradshaw & Main 1968).

In a comparative study of three species of chat (*Ephthianura*) which live in progressively drier habitats, G K Williams showed that behavioural and physiological traits changed in a way that paralleled the environmental changes associated with the different habitats occupied (Williams & Main 1976, 1977).

Macropods

While the foregoing research on frogs was proceeding, Professor Waring was in receipt of supporting funds from CSIRO for his studies of reproduction of marsupials. These studies concentrated on the reproductive physiology of the quokka (*Setonix brachyurus*) and the Tammar wallaby (*Macropus eugenii*), and it was during this time that studies on the ecology of marsupials was begun (Main, Shield & Waring 1959). These ecological studies focused on the ability of kangaroos and wallabies to survive periods of drought when water was scarce and available food was of poor nutritional quality. A preliminary study by me showed that the nitrogen levels in the gut contents of the quokka on Rottnest exceeded what could be expected even with the most favourable selection of dietary items, and suggested that the quokka might have a ruminant-like digestive system and thus would be capable of recycling urea. This supposition was confirmed by Moir *et al.* (1956). These observations led to further studies of dietary composition, water metabolism and urea recycling in kangaroos and wallabies.

Analysis of dietary composition was undertaken by G Storr, who used leaf epidermis to identify plant species eaten by the quokka, red kangaroo and the euro (Storr 1964, 1968).

E H M Ealey, then of CSIRO Wildlife Section, had begun a study of the euro (*Macropus robustus*), then regarded as a pest of the pastoral areas in the Pilbara. I was asked for assistance and advice based primarily on knowledge of the ecology of the quokka on Rottnest Island, which I regarded as a model of how a macropod adapted to aridity. I believed this to be so because, in its typical range, the quokka occupied mesic situations whereas on Rottnest its habitat was considerably more arid.

Later, as the work on the euro developed, I was quizzed by the head of the Wildlife Section on what I was doing and where it might lead. I explained to him that I believed that an understanding of the water and dietary needs of the euro were basic to any understanding of the ecology of the species in the arid area in which it occurred. From his comments I was left in no doubt that what I was proposing was a nonsensical vision, certainly lacking in any basis in classical ecology and with no hope of contributing to an understanding of field observations. Moreover, it was likely to be unproductive in the sense that it would not lead to an understanding of how kangaroos could live in such an inhospitable environment and particularly how the species could achieve such a pest status when available forage could not support sheep. In the event financial support continued and led to papers on field ecology of the euro (Ealey & Main 1967), diet (Storr 1968), water metabolism (Ealey *et al.* 1965) and nitrogen requirements (Brown & Main 1967). In essence, this work showed that the euro could supplement the low nitrogen of its diet by recycling urea.

Meanwhile, work continued on other macropods, especially the tammar wallaby whose ability to persist and thrive in dry habitats is well exemplified by its occurrence on East and West Wallabi Islands of the Abrolhos. These studies dealt with the ability to drink sea water

(Kinnear *et al.* 1968; Purohit 1974), recycle urea (Kinnear & Main 1975), and water and electrolyte metabolism (Bakker *et al.* 1983). A general interpretation of this work in terms of nutritional biology of ruminant and ruminant-like mammals was developed (Kinnear *et al.* 1979) and related to niche theory (Kinnear & Main 1979).

These studies were reviewed in the context of native animals as resources (Main 1969), measures of well-being (Main 1971; Bakker & Main 1980) and adaptations to desert conditions (Main 1975; Main & Bakker 1981), and as a factor in the Late Pleistocene extinctions of marsupials (Main 1978). A wider more generalised review (Main 1983) indicated a possible integration of macropod ecophysiology with ecological and evolutionary studies in the context of either the fundamental or realised Hutchinsonian niche (Hutchinson 1957).

The fundamental niche is an n -dimensional space which encloses all the environmental states that a species can tolerate and persist in indefinitely. In the presence of other species with which there are biological interactions, a species occupies a realised niche in which the dimensions are less than those of the fundamental niche. In the context of ecophysiology of macropods, these dimensions relate to heat tolerance (including reflective pelage), water balance, electrolyte metabolism, ability to recycle urea (supplement dietary nitrogen), and behavioural traits related to environmental structure (shelter and cover) which permit trade-offs between attributes of the niche and persistence in the unpredictable Australian environment. In the absence of other interacting species, the realised niche may approximate the fundamental niche. This is important in cases of single species on islands or in reservations where species may persist in quite atypical habitats because they still satisfy the dimensions of the fundamental niche *e.g.* quokka on Rottnest. Furthermore, when species are observed under field conditions, we see only the dimensions of the realised niche which may be a poor basis for prognosis of persistence or success in reservations where the ecosystem is changed and perhaps simplified.

The findings arising from the studies on macropods, birds and reptiles have converged to show that nutrition, dietary composition, water and electrolyte balance coupled with behaviour conspire to provide a suite of labile adaptations which permit survival when the environment in which the animals found themselves offered the scope to display and exploit the evolved traits.

These findings are relevant to conservation and raised questions of what could be retained in reservations. A question I had earlier (see below) approached from the point of view of adequacy of reserve size using macropod species retained on continental islands as a surrogate measure. However, the studies mentioned above raised questions other than simple size as contributing to persistence. For example, habitat structure, composition, senescence and regeneration appeared to be critical to maintain the habitats which gave scope for adaptive traits to be deployed. While these studies indicated requirements necessary for persistence of macropods, they also hinted at another problem, namely, whether management for the successful retention of nominated species (flagship or umbrella species) would ensure that other elements of the biota were also be retained.

Conservation

Like my other biological interests my concern with conservation dates back to my youth and as a member of the West Australian Naturalists Club.

While in the Army I had been stationed on the sand plains west of Dandarragan and had become very aware of the immense floral and invertebrate species richness of these areas. In 1947 I attempted to have extensive sandplain areas reserved but without success. The consensus opinion at the time was that these areas could not be used for agriculture and so would always remain as vacant crown land, and having them reserved would merely preclude other better areas from being considered for reservation. The fallacy of this reasoning became apparent as soon as it was realized that the agricultural potential could be enhanced simply by applying trace elements to the land.

My next direct involvement in conservation occurred when I set a student project on the Western Swamp Tortoise (*Pseudemydura umbrina*). This was taken up by Andrew Burbidge as the topic of a doctoral dissertation. Again, taxonomic relationships were crucial in obtaining a perspective for its conservation (Burbidge *et al.* 1974). Many subsequent observations by Burbidge have led to an understanding of the difficulties associated with conserving small populations of vertebrates.

In the 1950's, I had become associated with the Fauna Advisory Committee, later to become the Western Australian Wildlife Authority, which had the statutory responsibility for nature reserves under the Fauna Act. Initially the committee and the Authority advocated that no interference with reserves equated to good management of them *i.e.* leave Nature alone.

To me, reservations posed several problems;

- 1 there was no evidence that the size of the reserves being set up would fulfil the purpose for which they were being created especially whether they were adequate in area to maintain the biota included;
- 2 whether the disturbance resulting from fire and consequent plant successional pattern would permit the persistence of animals for which the reserves were being set aside;
- 3 whether the changed biotic environment *e.g.* within reserves, would permit the display of evolved traits and behaviour which laboratory and field analyses had demonstrated were a pivotal part of adaptation to the present environment.

At this time, even as at present, the species around which conservation efforts centred were vertebrates, usually marsupials and birds. In the absence of a long record of successful conservation within reservations, there was no way of directly establishing how large an area would retain one or more species of mammal. However, numerous islands around the Western Australian coast retained macropod marsupials since their isolation from the mainland by rising sea levels at the beginning of the Holocene. These islands offered a surrogate measure of the number of species of macropods which could exist on islands of various sizes for up to 11 000 years. Main (1961) and Main & Yadav (1972) argued that these data provided the only evidence for

predicting what could be retained in reservations of restricted size, assuming they were the analogue of islands.

The quokka on Rottnest and the tammar on the Abrolhos could persist in harsher, much more simplified environments than that usually occupied on the mainland, provided that the animals could exploit their behavioural and physiological repertoire of adaptive traits *i.e.* the environment remained within the dimensions of the species' fundamental niche. Thus, the prognosis was that the populations would persist in reserves of equivalent size. Unfortunately this first approximation underestimated the significance of the fox.

When setting aside land for reservation, it was hoped that marsupials, with their readily identified public appeal, would act as umbrella species beneath which other elements of the biota (plants and other animals, especially invertebrates) would be sheltered and so retained along with the high profile or principal species.

Notwithstanding the persistence of macropods on islands, it was clear from personal familiarity that the habitats available on an island are quite unlike mainland habitats in which the species now occurs and which were presumably like the ancestral ones. It is conceivable that proximity to the sea, salt spray, and exposure to high winds and storms may have changed the composition of communities. However, reserves in the wheatbelt landscape are also isolated and exposed, and retention of macropods in them was no guarantee that other elements of the biota initially included with them in a reserve would be also retained. This in turn suggested that a reserve management policy based on 'leaving Nature alone' was unlikely to be successful, particularly if macropods, or other charismatic species, were used as umbrella species in the hope of retaining other elements of the biota. Despite these quibbles, the islands around the Western Australian coast do indicate that retention of the original biota is dependent on island area. Large islands such as Bernier, Dorre and Barrow have not only retained macropods but also most resemble the mainland with respect to composition of the vertebrate biota prior to the arrival of the red fox.

The foregoing highlighted the need for understanding the dynamics of populations, communities and ecosystems, and particularly the role of disturbance, especially fire and herbivory, in their maintenance and regeneration. In the absence of the formerly wide-spread burrowing marsupials, rabbits and fire now tend to be the commonest agents causing disturbance and inhibiting plant regeneration. However, invertebrates such as grasshoppers may also exert subtle influences such as inhibiting the post-fire regeneration of jarrah trees by eating seedlings at the cotyledon stage (Whelan & Main 1979). This result emphasised how much the judgment that, 'it is reasonable to assume that insects are much less significant than grazing mammals in determining floristic composition', depends on our level of ignorance. An approach to the management of reservations in the Wheat belt of Western Australia was proposed by Main (1987).

In the early 1970's, I accepted appointments to the Universities Commission, the Council of the Australian Institute of Marine Science, and I was one of the initial

three members of the Western Australian Environmental Protection Authority. These appointments precluded extensive field work and my research emphasis changed as other issues emerged.

Important among the emerging issues were:

- (a) the potential for climatic change, under the influence of the greenhouse effect as atmospheric composition changed, to alter the structure and composition of biota retained within reserves;
- (b) an acceleration of salt encroachment in the wheatbelt landscape;
- (c) a developing appreciation of the significance of patches of remnant vegetation in maintaining a hydrological balance (many of these patches may be reservations for conservation purposes);
- (d) an appreciation of the necessity to develop concepts which would guide management practices rather than offer universal prescriptions for action.

In a very important sense, these issues all have a bearing on what can be retained within or outside reservations because they determine components of the realized niche of those species which are of concern for conservation. But the problem of establishing what species can persist is experimentally intractable over the period available for meaningful action to ensure retention.

The fundamental niche will only change slowly under the influence of selection; however, the realized niche will change whenever environmental conditions alter. Thus, should changes occur it is unlikely that the present composition will be retained because each species is likely to have a new realized niche resulting in the reorganisation of ecosystems. Notwithstanding these limitations, it seems likely that the insights gained from the studies reviewed above offer useful guidance in each of the fields listed. These have been applied in relation to ecosystem management (Main 1981a, b, c), and management of remnants of native vegetation (Main 1987), retention, significance and problems in retaining of rare species (Main 1982, 1984), fire tolerance of animals (Main 1981b), the role of biodiversity (Main 1992), climatic change and its likely effect on nature conservation (Main 1988), and restoration ecology (Main 1993).

Concluding Remarks

In the introduction, I set out how the lecture was to develop *i.e.* it was to be an illustration of how my natural curiosity posed the way in which questions were asked and how these led to matters of conservation. It is now possible to draw the lessons together and in doing this I wish to emphasise the close relationship of biology, politics and society.

The core of science is; recognise entities; distinguish them from similar entities; classify; explain *i.e.* have an hypothesis and then test it. The first step is to distinguish and describe entities so that others can recognise them. Should recognition not be precise then the use of the entities in experiments *e.g.* taking sibling or cryptic species together as one entity will mean that comparative studies will be handicapped.

But there is a more general point to be made with regard to classification. I have been, or am regarded (classified) as a herpetologist (I admit that being an elected Honorary Life Member of the American Society of Ichthyologists and Herpetologists must colour the interpretation) but the initial choice of frogs for study was my familiarity with them and a belief that they would be a satisfactory experimental animal for study of adaptations to aridity. This last theme is the key to my work on frogs. Moreover, the pursuit of a problem or theme across disciplinary (taxonomic) boundaries *i.e.* a comparative approach, is the only way to test the generality of an interpretative hypothesis which in the present case was that physiology, behaviour in an environment which permitted the display of evolved physiological and behavioural responses provided the basis for survival of individuals and persistence of populations. The survival of organisms during periods of drought and aridity experienced in the past and their capacity to persist in restricted areas and as small populations during such times (including post-fire situations) is likely to have selected traits that are adaptive under such conditions. Study of such past events and population consequences is relevant to conservation where persistence as small populations in restricted areas is the central problem to be solved. But this is an example of seamless Nature; the call now is for teams to undertake interdisciplinary studies in order to solve a problem. The problem may be well defined and pressing; however, there is often an absence of theory on which testable hypotheses can be erected. Additionally, it is often not clear that a need for theory is appreciated, the vision of what is to be studied is purely practical, applied and constrained by utilitarian goals. The current funding sees the study of Nature as being that of patches of fabric which can be stitched or cobbled together to serve utilitarian purposes. This result is the logical end point of the comments received by me and referred to above regarding my disrespect for, and transgression of, the currently accepted disciplinary boundaries, namely that knowledge of the world about us is hopelessly fragmented.

Of course the initial choice of questions to be addressed in my research was not a scientific one. It may be conceived as morally proper to know and understand the surrounding world but the decision of what to study and how to proceed was a personal choice, only the methodology was scientific. Yet, as mentioned earlier, the crossing of perceived boundaries did receive some comment, which can be interpreted in two ways;

- 1 that the accepted boundaries should be taken as given and not transgressed;
- 2 the decision by me to try and understand the surrounding world was morally wrong. A proper approach was to stay within boundaries and/or to address problems posed by society *i.e.* deal with applied problems where a need for cross disciplinary work may be demonstrated.

Thus the current approach of assembling teams formalises, in an administrative sense, the personal prejudices so frequently expressed in the past *i.e.* synthesis is only needed when practical solutions demand it. The broad understanding and interpretation is seen as unnecessary; it is only needed to satisfy the pragmatic

requirements of cost effective economic progress *e.g.* to ensure 'the sustainable utilisation of ecosystems and species' (Anon 1987).

More broadly, the foregoing is often taken to mean retaining biodiversity (species richness) and ecosystem functions. Taking the ecosystem functions to embrace responses to competition, disturbance, and stress (Grime 1974) and recognising the physiological and behavioural requirements of species for their survival poses the question of the nature of the assumption being made about environmental stability. At its simplest, the assumption is that the present is like the past and the future will be likewise. Historical geological considerations suggest that this is unlikely. Moreover, conditions are changing rapidly with development which is leading to more radical changes than occurred in the past; it is unlikely that the future will be like the present. Thus we are left with the question of whether the physiological, nutritional, and life history and behavioural traits of species (their fundamental niches) can be satisfied in the new environments. These are management problems and successful outcomes depend on decisions being made promptly, but with recognition that adaptive management in the sense used by Walters (1986) may be called for. This is a condition that is rarely met because there is a perception that there should be complete understanding before action is taken or decisions made. This desire for certitude is, however, often eclipsed by a desire on the part of administrators to achieve or maintain status or exercise sheer power which would be entirely appropriate in the jungles of the natural world. The general difficulties experience by ecologists when dealing with decision-makers have been discussed by me (Main 1996). Despite the traumas and difficulties associated with involvement in arriving at, or implementing, decisions it behoves ecologists to become involved in the way their knowledge is used, without their presence when decisions are made ecological knowledge will be misconstrued, misinterpreted or ignored in both conservation problems and environmental issues. I regard discovery, interpretation and application of information as the result of a conscious decision as being the political manifestation of the seamlessness of Nature.

Acknowledgments: It is a pleasure to acknowledge; financial support from the University Research Grants committee, The Australian Research Grants Committee, and from CSIRO funds to Professor H Waring; the co-operation and tolerance of my co-workers; the generous assistance and help from many in organisations outside the University which made it all possible. I am grateful for the Honorary Research Fellowship in the Zoology Department, University of Western Australia.

To the extent that I have succeeded in the pursuit of my vision I have been favoured by luck in being in the right place at the right time. To all those who made it possible, especially my wife Barbara York Main, I am extremely grateful.

It has been wonderful for me to pursue my hobby. I am sure I could not do so in the present economic and funding climate.

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Diurnal stratification of Lake Jandabup, a coloured wetland on the Swan Coastal Plain, Western Australia

D S Ryder & P Horwitz

Department of Environmental Management, Edith Cowan University, Joondalup WA 6027

Manuscript received June 1995; accepted February 1996

Abstract

Variations in temperature and dissolved oxygen gradients were examined for three microhabitats in Lake Jandabup over a 24 hour period in 1993; each microhabitat was thermally stratified between 1300 and 1900 hrs. The presence of a shallow water column (< 0.5m) that is shown here to stratify thermally under a known set of conditions has implications for sediment nutrient release, insufficient oxygen supply for aerobic organisms and an accumulation of organic sediments.

Introduction

The presence of dissolved humic substances in aquatic systems can influence the physical and chemical characteristics of the standing water (Kuuppo-Leinikki & Salonen 1992), causing the rapid attenuation of solar radiation at shallow depths (Bowling *et al.* 1986) and producing steep thermal gradients that are resistant to mixing (Bowling 1990). Literature regarding the stratification of Australian inland waters is dominated by studies of large and/or deep lakes and reservoirs (e.g. Bowling 1990) with Western Australian literature also having these emphases (e.g. Imberger 1985). Recent work has highlighted the stratification of coloured or saline waters in southwestern Australia. For instance, Edward *et al.* (1994) found many coastal wetlands in the extreme southwest to be thermally stratified, while Burke & Knott (1989) demonstrated that saline Lake Hayward in Yalgorup National Park was monomictic. Schmidt & Rosich (1993) examined stratification and thermal stabilities of Swan Coastal Plain wetlands, concluding that only deep (>3m) or highly coloured wetlands would stably stratify. However, Burke & Knott (1989) showed that stratification can be achieved in shallow lakes, provided that there was sufficient salinity difference between the upper and lower water layers.

The aim of this study was to examine diurnal fluctuations in temperature and dissolved oxygen gradients over a 24 hour period during autumn in Lake Jandabup.

Methods

Lake Jandabup occupies a shallow (<1.5 m), oval-shaped basin, 22 km north of Perth on the Swan Coastal Plain (Allen 1979). The littoral zone is dominated by *Baumea articulata* (R Br) ST Blake (jointed twig rush) and other rushes with *Typha orientalis* C Presl (bulrush) limited to isolated pockets within the lake (Froend *et al.* 1993).

The study sites 1, 2 and 3 (see Ryder & Horwitz 1995) were within vegetation communities dominated by *B.*

articulata, *T. orientalis* and a community with no emergent or submerged vegetation respectively. Dissolved oxygen (DO; % saturation) and temperature (°C) were recorded at two hourly intervals *in situ* on March 20 to 21, 1993, over a 24 hour period using a portable *Wissenschaftlich Technische Werkstätten* Oximeter. Measurements were made at the top (5 cm below water surface) and bottom (epibenthic) of the water column. Ambient air temperature and wind data were obtained from the Bureau of Meteorology.

Results

Water depths at sites 1, 2 and 3 were 0.449 m, 0.404 m and 0.453 m respectively. The maximum air temperature on site was 26.5°C at 1500 hours and the minimum of 13.1°C was recorded at 0500 hours. Wind data are shown in Fig 1.

A thermal gradient was present between the top and bottom of the water column at all sites between 1300 and 1900 hours. Sites 1 (*B. articulata* community), and 2 (*T. orientalis* community) exhibited the greatest differences between surface and epibenthic temperatures, of 6.6°C and 6°C respectively (Fig 1). Site 3 (open water) had the highest surface temperature of 24.1°C; however, only a 3.4°C maximum temperature difference was evident. All sites displayed low epibenthic oxygen saturation while surface water remained well oxygenated. Site 1 had the lowest epibenthic DO level of 0 % saturation. Site 2 displayed similar, although slightly higher values. Site 3, which was exposed to the prevailing winds more so than the other sites, had a surface oxygen level reaching 128 % saturation at 1700 hours, with epibenthic DO levels of 11 % saturation.

Discussion

This study has demonstrated the potential for the daily thermal stratification of Lake Jandabup, despite its shallow water depth and relatively high surface area. The climatic conditions, particularly the wind pattern, were typical of summer and autumn conditions experienced on the Swan Coastal Plain (Gentilli 1972). This

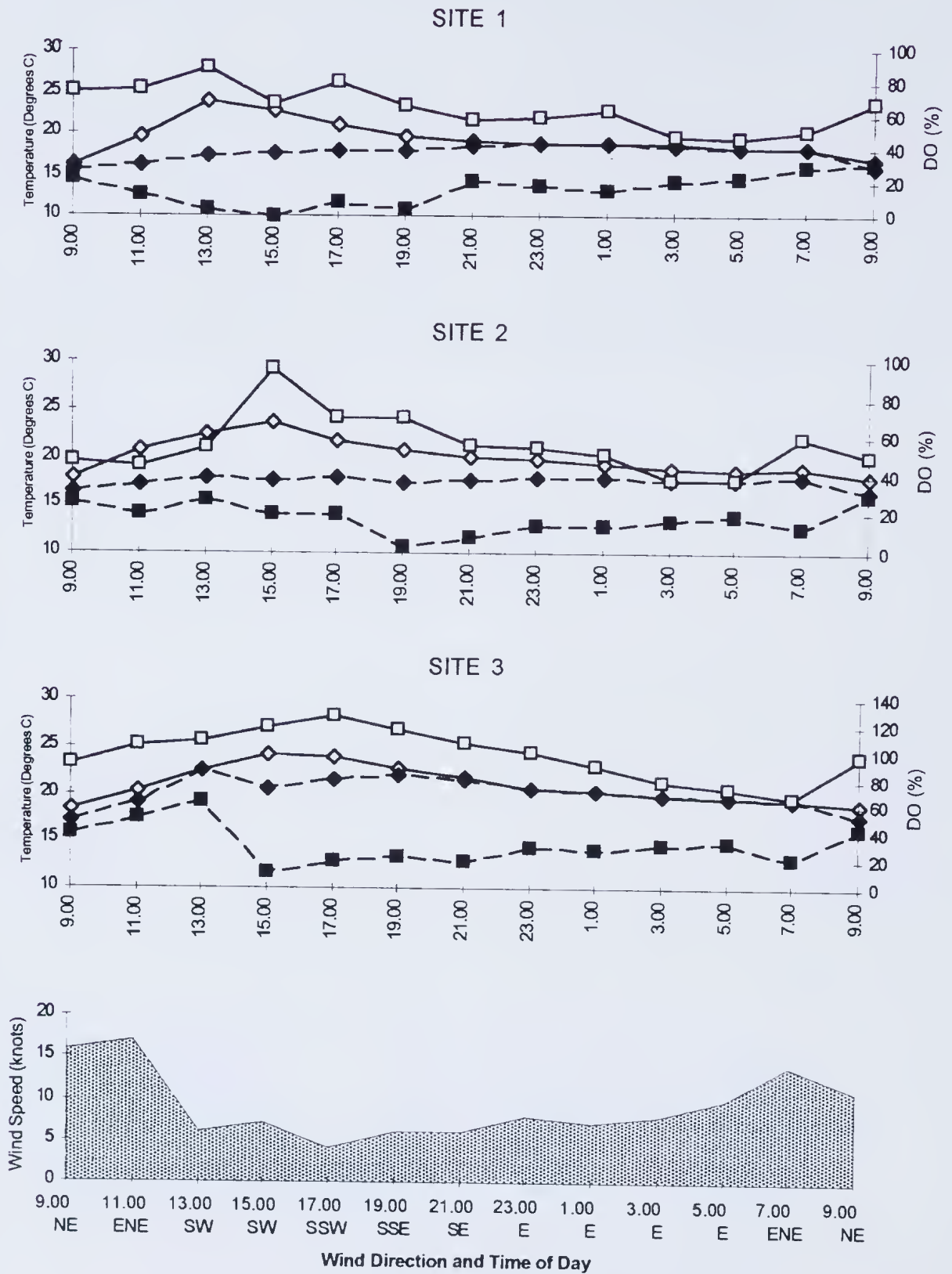


Figure 1. Temperature (°C) and DO saturation (%) readings for the top and bottom of the water column at sites 1, 2 and 3, and windspeed and direction over the 24 hour study period from 20 to 21 March 1993. Temperature top $\diamond$, temperature bottom $\blacklozenge$, DO top $\square$, DO bottom $\blacksquare$.

pattern of daily stratification could therefore be expected to occur regularly over a six month period.

Surface and epibenthic temperature differences and epibenthic deoxygenation were most pronounced in the dense *B. articulata* community and least evident in open water. As the major mixing force in wetlands is produced by the shearing effect of the wind at the water surface (Schmidt & Rosich 1993), it appears that the emergent vegetation may be limiting the input of atmospheric oxygen as well as providing shelter and resistance to mixing. Wetlands such as Lake Jandabup, with large areas of emergent vegetation and coloured water may therefore have an exacerbated daily and seasonal cycle of thermal stratification.

Based on traditional limnology (e.g. Wetzel 1983), wetlands such as Lake Jandabup would be classified as warm polymictic, based on the temperature, climate and basin geomorphology. However, despite the obvious shallowness of Lake Jandabup, the presence of a water column that has been shown to stratify thermally under a known set of conditions requires the wetland to be classified as warm continuous monomictic.

The presence of a stratified water column based on thermal profiles is supported by differences in surface and epibenthic DO levels. These DO differences are most pronounced during the period of thermal stratification, but persist throughout the 24 hour period due to the atmospheric diffusion of oxygen through the water column being unable to supply the high oxygen demand of the organic soils present in the lake. This has implications for sediment nutrient release, insufficient oxygen supply for the metabolic requirements of aerobic organisms, and an accumulation of organic sediments in Lake Jandabup and other similar wetlands on the Swan Coastal Plain.

Acknowledgments: We would like to thank Mr Doug Ryder and Mr Allan Ellies for their help in the field.

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Cocoon formation by the treefrog *Litoria alboguttata* (Amphibia: Hylidae): A 'waterproof' taxonomic tool?

P C Withers¹ & S J Richards²

¹ Department of Zoology, The University of Western Australia, Nedlands, WA 6907

² Department of Zoology, James Cook University, Townsville, QLD 4811

Manuscript received June 1995; accepted January 1996

Abstract

The hylid frog *Litoria alboguttata* (formerly *Cyclorana alboguttatus*) forms a cocoon during aestivation. After 21 days of water deprivation a thin, transparent cocoon is formed; the cocoon covers and closely adheres to the entire body surface, except the external nares. The cocoon consisted after 21 days of about 24 layers of squamous epithelial cells, about 14-18 μ thick. It reduced markedly the rate of evaporative water loss (measured at 22 °C) from 39.3 mg g⁻¹ h⁻¹ (non-cocooned frogs) to 2.1 mg g⁻¹ h⁻¹ (cocooned frogs). The formation of a cocoon by *Litoria alboguttata* raises the question of the possible phylogenetic significance of cocoon formation amongst the Australopapuan frogs, because no other *Litoria* has yet been reported to form a cocoon but cocoon formation is common amongst both *Cyclorana* and *Neobatrachus*. Cocoon formation may have independently arisen at least three times amongst Australopapuan frogs (*Litoria*, *Cyclorana*, *Neobatrachus*). Alternatively, *Litoria alboguttata* may be more closely allied with *Cyclorana* than *Litoria*, or cocoon formation was a primitive capability of the frogs ancestral to both *Litoria* and *Cyclorana*, and so cocoon formation independently evolved only twice in Australopapuan frogs.

Introduction

This study was prompted by the report of Lee & Mercer (1967) that *Litoria alboguttata* (called *Cyclorana alboguttatus* by them) form a cocoon; they also reported that *Cyclorana platycephala*, *C. australis*, *Neobatrachus pictus* and *Limnodynastes spenceri* form a cocoon. The cocoon of these frogs, and of a number of other non-Australian frogs (*Pyxicephalus*, *Leptopelis*, *Lepidobatrachus*, *Ceratophrys*, *Pternohyla*, *Smilisus*) is a multi-layered covering of sloughed skin formed during aestivation; it markedly reduces evaporative water loss (Loveridge & Crayé 1979; McClanahan *et al.* 1976; Ruibal & Hillman 1981; McDiarmid & Foster 1987). Since the pioneering study of Lee & Mercer (1967), cocoon formation has been described for a variety of species of *Cyclorana* (van Beurden 1982; Withers 1995; Richards, unpublished observations) and *Neobatrachus* (Withers 1995), but cocoon formation has not been observed for *Limnodynastes spenceri* (Withers, unpublished observations) and there have been no further studies of cocoon formation by *Litoria alboguttata*.

Cocoon formation by *Litoria alboguttata* is of particular interest because the taxonomic position of *Litoria alboguttata* within the monophyletic *Cyclorana* or *Litoria aurea* species group is problematical (Tyler & Davies 1993). The Australopapuan hylid frogs (Hylidae, Pelodyadinae: *Cyclorana*, *Litoria* and *Nyctimystes*) appear to be a monophyletic group (Tyler 1979; Hutchinson & Maxson 1987; Tyler & Davies 1978, 1993), but only relatively few of the species have been considered in phylogenetic analyses within the taxon. *Litoria alboguttata* was described as *Chiroleptes alboguttatus* Gunther (1867); it was moved to *Mitrololysis* by Cope

(1889) and then to *Cyclorana* by Parker (1940). Tyler (1973) considered it to be a species of *Litoria* and a member of the *Litoria aurea* complex, as *L. alboguttata*.

The objectives of this study were to confirm that *Litoria alboguttata* formed a cocoon during aestivation, to examine the structure of the cocoon, and to measure the rate of evaporative water loss of normal and cocooned frogs.

Methods

Twelve specimens of *Litoria alboguttata* were collected at Townsville, Queensland, and transported to Perth for study (two frogs are deposited in the WA Museum as voucher specimens R119533, R119534). Initially, the frogs were maintained individually, in the dark, with access to free water, in plastic containers that had a small hole in the lid for gas exchange. After initial measurements were made for hydrated frogs, no free water was provided and the frogs were slowly dehydrated to induce cocoon formation. Frogs were maintained, and all experiments conducted, at room temperature (approx. 22 °C).

The rate of evaporative water loss (EWL) was determined by flow-through hygrometry. EWL was first measured at the start of the study for control, hydrated frogs, and then at the end of 21 days of dehydration for cocooned, aestivating frogs. Each frog was weighed to $\pm$ 0.001 g and then placed in a vertically-oriented glass tube (5 cm diameter) on a plastic mesh platform. Compressed dry air (dewpoint = -10 °C) was passed at a flow rate of 2000 ml min⁻¹ through the tube and then a General Eastern model 1100A dewpoint hygrometer. The analog voltage output of the hygrometer was monitored by a Thurlby 1905a digital multimeter, and its RS232 output was interfaced to a PC. The excurrent

dewpoint was monitored at 30 sec intervals, and converted to relative and absolute humidity using the equations of Parrish & Putnam (1977). The absolute evaporative water loss rate (EWL; mg min^{-1}) and mass-specific evaporative water loss (MSEWL; $\text{mg g}^{-1} \text{h}^{-1}$) were calculated from the air flow rate, incurrent and excurrent absolute humidity, and body mass. The surface-area-specific evaporative water loss (SAEWL; $\text{mg cm}^{-2} \text{h}^{-1}$) was calculated assuming a surface area (cm^2) of 9.9 $\text{grams}^{0.567}$ (McClanahan & Baldwin 1969). Total resistance to evaporative water loss ($R = \Delta C / \text{SAEWL}$; sec cm^{-1}) was calculated from SAEWL (converted to $\mu\text{g cm}^{-2} \text{sec}^{-1}$), assuming the difference in water vapor concentration (ΔC ; $\mu\text{g cm}^{-3}$) driving evaporation was the difference between absolute humidity for saturated air at 22 °C and the incurrent absolute humidity.

Samples of cocoon were removed from aestivating frogs, and examined by scanning and transmission electron microscopy. For scanning electron microscopy, air-dried samples and glutaraldehyde-fixed samples of skin were mounted on an aluminium stub using double-sided adhesive tape, and sputter-coated with gold-palladium. The thickness of the cocoon was determined using the air-dried specimens, and the number of layers counted using the glutaraldehyde-fixed specimens. Specimens were examined using a Phillips 505 scanning electron microscope.

Samples of air-dry cocoon were prepared for transmission electron microscopy by fume fixation with osmium tetroxide and direct embedding in araldite. Ultrathin sections were cut and stained with uranyl acetate and lead citrate. Specimens were examined using a JOEL FX2000 transmission electron microscope.

All experiments were conducted with the approval of the Animal Ethics Committee, University of Western Australia.

Results

All frogs were hydrated and healthy at the start of the study, when EWL was determined for all individuals, and then were water-deprived. Most specimens of

Litoria albobuttata became quiescent, adopted the water-conserving posture, and commenced cocoon formation (Fig 1) within 7 days of the start of water deprivation. A well-developed, transparent cocoon was apparent after 21 days, when EWL was redetermined and the cocoon was removed for microscopical examination. At this time the cocoon was a thin, transparent sheet that covered and closely adhered to the entire body surface, including the closed eyes, mouth and cloaca. Only the external nares were free of the cocoon, to allow pulmonary ventilation. The cocoon was easily peeled from the skin; the freshly-exposed skin appeared and felt moist.

The piece of cocoon examined by scanning electron microscopy consisted of about 24 discrete layers (Fig 2A) forming a compact sheet (Fig 2B) approximately 14–18 μ thick; each layer is consequently calculated to be about 0.6–0.7 μ thick. A transmission electron micrograph of the cocoon (Fig 3) more clearly shows the individual electron-dense cell layers, about 0.7 to 1.0 μ thick, separated by 0.1 to 0.2 μ thick inter-cellular spaces. The outer surface of the cells is more crenulated than the inner surface. Inter-cellular junctions are evident in some of the layers.

The mean body mass of *L. albobuttata* was $20.6 \pm \text{se}$ 0.7 grams ($n=9$). The rate of evaporative water loss declined markedly from 13.4 mg min^{-1} for non-cocooned *L. albobuttata* ($39.3 \text{ mg g}^{-1} \text{h}^{-1}$; $4.07 \text{ mg cm}^{-2} \text{h}^{-1}$) to 0.74 mg min^{-1} for cocooned frogs ($2.1 \text{ mg g}^{-1} \text{h}^{-1}$, $0.22 \text{ mg cm}^{-2} \text{h}^{-1}$; Table 1). The resistance was considerably higher for cocooned frogs (89.4 sec cm^{-1}) than non-cocooned frogs (3.1 sec cm^{-1} ; Table 1).

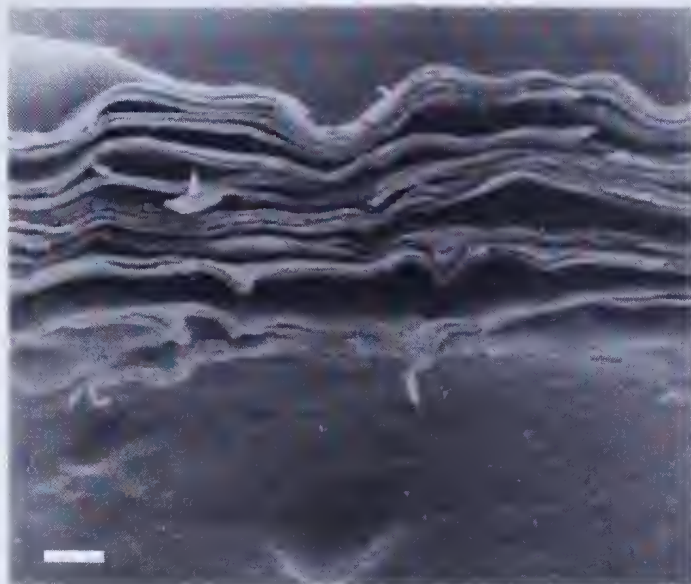
Table 1. Evaporative water loss for hydrated and cocooned *Litoria albobuttata*. Values are mean $\pm$ standard error; n is the sample size. All values for cocooned frogs are significantly different from the values for control frogs, by t -test ($P < 0.05$).

	Hydrated($n=9$)	Cocooned($n=6$)
Absolute EWL (mg min^{-1})	13.4 ± 0.6	0.74 ± 0.12
Mass-specific EWL ($\text{mg g}^{-1} \text{h}^{-1}$)	39.3 ± 2.0	2.1 ± 0.3
Surface-area-specific EWL ($\text{mg g}^{-1} \text{h}^{-1}$)	4.1 ± 0.2	0.22 ± 0.03
Resistance (sec cm^{-1})	3.1 ± 0.3	89.4 ± 14.9



Figure 1. An aestivating *Litoria albobuttata* in the water-conserving posture and covered with a transparent cocoon that covers the entire outer body surface (including eyes, mouth and cloaca) except for the openings of the nares.

A



B

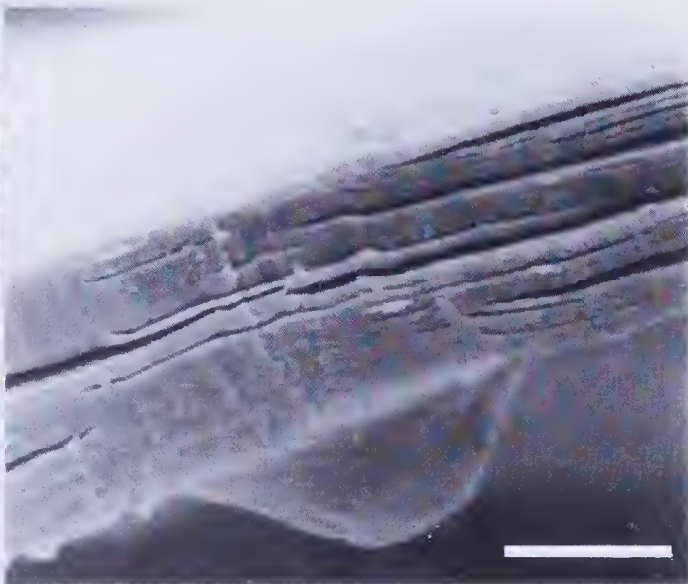


Figure 2. Scanning electronmicrographs of the cocoon of *Litoria alboguttata*. A. glutaraldehyde-fixed specimen showing individual layers B. an air-dried specimen showing the compact *in vivo* structure of the cocoon. Scale bars are 10 μ .

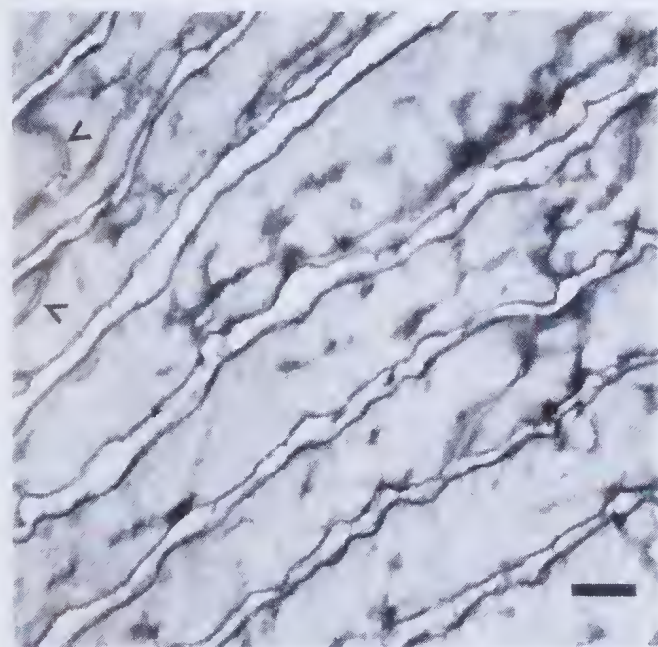


Figure 3. Transmission electronmicrograph of an air-dried specimen of *Litoria alboguttata* cocoon, showing detail of squamous cells and intercellular space. Imbricate intercellular junctions are indicated by arrow heads. Scale bar is 500 μ m.

Discussion

It is clear from Lee & Mercer (1967) and this study that *Litoria alboguttata* forms a cocoon during aestivation; however, cocoon formation has not yet been described for any other species of *Litoria*. The general appearance and structure of the cocoon of *L. alboguttata* is similar to that of other Australian cocoon-forming frogs (*Neobatrachus* and *Cyclorana*; Withers 1995), and also *Pyxicephalus adspersus* (Parry & Cavill 1978; Loveridge & Crayé 1979), *Lepidobatrachus llanensis* (McClanahan *et al.* 1976), *Pteruohyla fodiens* (Ruibal & Hillman 1981) and

Smilisca baudinii (McDiarmid & Foster 1987). The thickness of individual layers of the cocoon of *L. alboguttata*, 0.6–0.7 μ , is more similar to that of *Neobatrachus* spp (0.57–0.62 μ) than *Cyclorana maini* (0.39 μ ; Withers 1995) but the rapid rate of cocoon formation for *L. alboguttata* (at least 1.1 layers d^{-1}) is more similar to that of *C. maini* (0.57 d^{-1}) than *Neobatrachus* spp (0.22–0.35 d^{-1} ; Withers 1995).

The cocoon of *Litoria alboguttata* significantly reduces its rate of evaporative water loss, as has been observed for other cocoon-forming *Cyclorana* spp, *Neobatrachus* spp, and other genera. The resistance to water loss (3.1 $sec\ cm^{-1}$) of non-cocooned *L. alboguttata* is slightly higher than that for typical 'non-waterproof' frogs and a free water surface (about 1 $sec\ cm^{-1}$). This might reflect an underestimation of evaporative surface area, a substantial resistance of the cutaneous boundary layer, or initial stages of cocoon-formation in some of the "non-cocooned" individuals (resistance ranged for non-cocooned individuals from 2.4 to 4.9 $sec\ cm^{-1}$). In contrast, the resistance to water loss of cocooned frogs was much higher, at about 90 $sec\ cm^{-1}$; such resistance values are typical for other species of cocooned frogs (Loveridge & Withers 1981; Withers, unpublished observations for *Cyclorana* and *Neobatrachus* spp).

Cocoon formation has presumably evolved independently at least three times in the Australopapuan frogs *i.e.* in both hylid genera *Cyclorana* and *Litoria* and the myobatrachid genus *Neobatrachus*. If *Litoria alboguttata* is ascribed to the *Cyclorana australis* species group as suggested by Maxson *et al.* (1982, 1985), then cocoon formation need only have evolved independently twice in Australopapuan frogs, once in *Cyclorana* (there is at least one cocoon-forming frog in each of the three *Cyclorana* species groups listed by Tyler & Davies 1993), and once in *Neobatrachus*. Or, if cocoon formation was a primitive capability of the common ancestor of both *Litoria* and *Cyclorana*, but has been subsequently lost in most *Litoria* spp, then cocoon formation need only have

evolved twice in Australopapuan frogs. However, the analyses of Maxson *et al.* (1982, 1985) suggest that *C. platycephala* is remote from its congeners (and *L. alboguttata*) and is allied with the *Litoria aurea* complex; if so, then cocoon-formation might have evolved independently in *C. platycephala* (or other members of the *L. aurea* complex also form cocoons but this has not yet been recorded, or they have lost the capacity to form a cocoon). The ability to form a cocoon, although it cannot be considered to be a taxonomic tool *per se*, provides suggestive evidence of a close phylogenetic relationship between *Cyclorana* and *Litoria alboguttata*, and it will be of interest to see if such a relationship holds when the patterns of cocoon formation and phylogenetic relationships are clearer for Australopapuan frogs.

Acknowledgements: We thank Tom Stewart for his major contributions to the histological work in this study, the Electron Microscopy Centre of the University of Western Australia for providing SEM and TEM facilities, and the Department of Conservation and Land Management for permission to import frogs into Western Australia. We are grateful to M Tyler and W Buttemer for constructive comments on the manuscript.

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Foraging patterns and behaviours, body postures and movement speed for goannas, *Varanus gouldii* (Reptilia: Varanidae), in a semi-urban environment

G G Thompson

Edith Cowan University, Joondalup Drive, Joondalup, WA 6027

Manuscript received July 1995; accepted February 1996

Abstract

Two Gould's goannas (*Varanus gouldii*) were intensively observed in the semi-urban environment of Karrakatta Cemetery, Perth, Western Australia. After emerging and basking to increase their body temperature, they spent most of their time out of their burrows foraging, primarily in leaves between grave covers, and under trees and shrubs. Mean speed of movement between specific foraging sites was 27.6 m min^{-1} , whereas the overall mean speed while active was only 2.6 m min^{-1} because of their slower speeds while foraging. A number of specific body postures were observed, including; vigilance, walking, erect, and tail swipes. Specific feeding and avoidance behaviours were also recorded, along with the influence that two species of birds had on their selection of foraging sites.

Introduction

Our knowledge of foraging habits, patterns, home range and activity area size, posture, and behaviour for large goannas has been extended since the early work of Cowles (1930) with *V. niloticus*, and Green & King (1978) with *V. rosenbergi*. Recent comprehensive studies include those by Auffenberg (1981a,b; 1988; 1994) for *V. komodoensis*, *V. bengalensis* and *V. olivaceus*, Auffenberg *et al.* (1991) for *V. bengalensis*, Daltry (1991) for *V. salvator*, and Weavers (1993) for *V. varius*. General descriptions of varanid locomotion, postures and foraging behaviour are given by King & Green (1993 a,b). However, there remains a paucity of data concerning the behaviours, body postures and movement patterns of small and medium sized varanid lizards.

Pianka (1994) reports that Australian desert goannas, such as *V. gouldii*, are exceedingly wary, unapproachable, and unobservable; this consequently makes it very difficult to study their use of time and space, foraging behaviour and body postures. Because *V. gouldii* at Karrakatta Cemetery have learned to accommodate to the presence of people, this site provides a unique opportunity for a study of their behaviour and foraging patterns that is not possible in more remote locations.

This study is the third in a series (Thompson 1992, 1994) on the movements, behaviours and ecology of *V. gouldii* at Karrakatta Cemetery, Perth, Western Australia. The earlier papers report on the daily distance travelled, foraging areas and the size of the activity area during the breeding season. The primary objective of this study was to examine in detail the behaviours, postures and preferred micro-habitat foraging sites for two particular individual *V. gouldii*.

Methods

Study Site

Karrakatta Cemetery (115° 47' E, 31° 55' S) is located within the Perth metropolitan area, approximately 4 km west-south-west of the city centre. It has 53 ha allotted to burial plots and another 53 ha to roads, ornamental gardens and buildings. The cemetery is planted with a range of exotic shrubs and trees, with many of the northern, central and eastern areas being grassed. There are numerous rose gardens to the south and east of the main entrance, which are located on the northern boundary (see Thompson 1992, 1994). A nature reserve of approximately 7 ha is located on the south-eastern boundary. The study site was located in the southern section of the cemetery (Fig 1).

Monitoring procedures

A miniature radio-transmitter with a battery life of approximately 140 days (11 g mass; TX1 1C temperature-pulse, Bio-Telemetry Tracking) was attached to the lateral aspect of the base of the tail for seven *V. gouldii* in early November, 1993. The radio transmitter was sewn into a denim harness that was glued with Selleys 'kwik-grip' to the skin of the goanna's tail to encircle the tail for a length of approximately 50 mm. Each goanna was located prior to observations commencing each day with a Bio-tel RX3 receiver operating in the 150-151 MHz band in conjunction with a 3EY directional antenna. The behaviour and daily movements of five of these *V. gouldii* were initially monitored to choose two goannas that readily adapted to being observed. Behavioural observations over five weeks commenced on these two *V. gouldii* [#1, a female, with a body mass of 330 g, snout-to-vent length (SVL) of 314 mm; and #2, a female, with a body mass of 348 g and SVL of 300 mm] on 1 December 1993 and concluded on 18 January 1994. This study was conducted in conjunction with a study that continuously

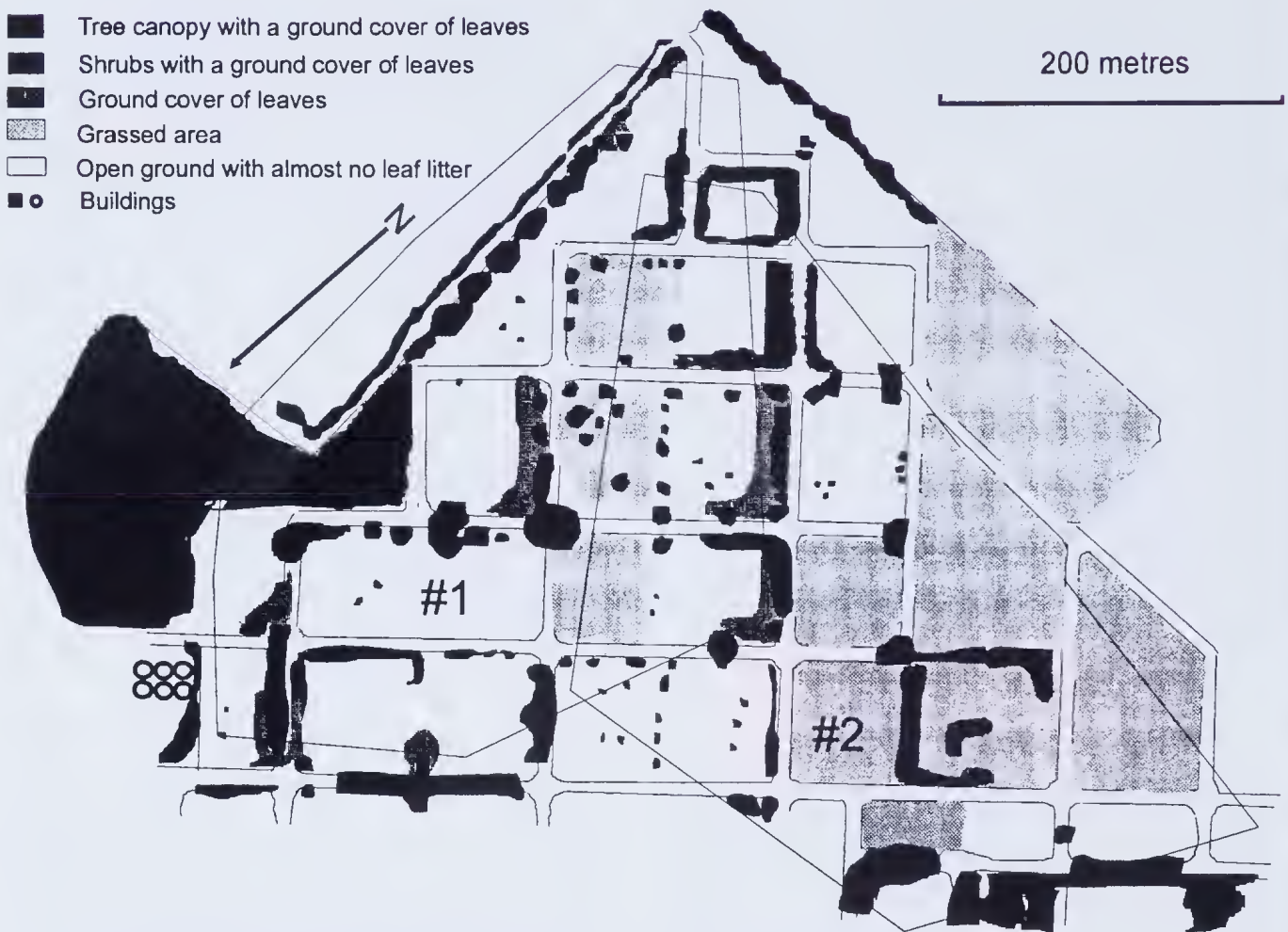


Figure 1. Karakatta Cemetery, showing the study site vegetation and *V. gouldii* activity areas.

monitoring of the body temperature of these *V. gouldii* over a number of months using temperature sensitive transmitters attached to the lizards and a data-logger connected to a large stationary antenna.

During the first week of observation, each goanna was initially monitored from a distance of approximately 50 m. After this adjustment period, most observations were then carried out from a distance of 15 to 35 m. On numerous occasions, the observed *V. gouldii* moved toward the observer, reducing the distance to observer to less than 5 m, and on a few occasions to less than 2 m. This suggests that the presence of an observer had a minimal influence on their behaviour. The data from the first week of observation of the two *V. gouldii* were not analysed, as this period allowed these two *V. gouldii* to adjust to the continued presence of an observer.

Two well trained observers spent a total of 131 hours watching and recording data for these two *V. gouldii* or waiting for them to emerge from their burrows, but they never spent more than half a day observing one goanna, to minimise any impact that these observations might have had on their normal behaviour. The recording procedures of the two observers were checked every couple of days during the first two weeks to ensure consistency of observations and recording of data.

Foraging, movement and posture recording procedures

Observations for each goanna on the choice of foraging site, general habitat, extent of exposure to the sun and distance moved were recorded for the previous nine minute interval in the categories shown in Table 1. Movement behaviour for each nine minute period was classified into seven categories (Table 1). Data reported for the micro-habitat of foraging sites, general habitat type selected, extent of exposure to the sun, and distance travelled, include only the time between when the goanna commenced foraging to when it either returned to a burrow or observations ceased (but excludes the time between when the goannas emerged from their overnight burrow and when they were first observed basking in the sun to increase their body temperature T_b). Goannas often moved through various sites during the nine minute period. The predominant environment for the period is the one reported. The number of times that *V. gouldii* #1 was seen to capture a prey item was also recorded, and is reported as the mean number of minutes between successful strikes. In addition, observers recorded the time when the goanna produced a scat, its behaviour and when the two *V. gouldii* were harassed by birds. Observers also noted the feeding and digging behaviours for these two goannas.

In late December, 1993, both goannas were recorded by video camera for a total of 6 hours, (four hours for

Table 1. Alternatives used to classify the foraging sites, general habitat, extent of exposure to the sun and movement behavior.

Micro-habitat foraging sites	General habitat type selected	Extent of exposure to the sun	Movement behaviour
Between grave covers	Between graves	Total sun	Emerging from an overnight burrow
Leaves under trees or shrubs	On top or the side of graves	$\frac{3}{4}$ sun	Basking but not moving
Under grave covers	Under grave covers	$\frac{1}{2}$ sun	Basking and moving
Leaves in an open area	Grassed areas	$\frac{1}{4}$ sun	Moving about outside a grave cover
Grass in an open area	On the road verge	All of the time in the shade	Moving under a grave cover
Grass under trees or shrubs	Treed areas	Under grave cover or in a burrow	Stationary and looking
	In the yards of adjacent houses		Avoidance (people, dogs, birds, vehicles)
	Up a tree		
	In the nature reserve (heavily grassed with $\approx 50\%$ tree canopy)		

one and two hours for the other), over a four day period and body postures were drawn from these video images. Reference to this visual record was also used to clarify the written descriptions of each observer for postural, feeding and digging behaviours.

The linear distance that each of the two *V. gouldii* moved during each nine minute observation period was estimated by recording the number of grave lengths and widths (3.6 m and 1.8 m respectively) that the goanna had passed during the period. This distance is a slight underestimate of the total distance moved due to the meanderings of the goannas while they foraged. However, as the goannas mostly moved between grave covers

or between foraging sites, their actual movement path was generally a series of near linear movements. These were summed for each period. For example, if a goanna was to circumambulate a grave cover the total linear distance would be approximately 10.8 m presuming it moved midway between adjacent grave covers. From these data, the mean distance travelled per minute was calculated. The average speed of movement between foraging sites was estimated by recording the time, to the nearest 0.1 second, that it took for a *V. gouldii* to cover a known distance (e.g. length of a grave plot) over thirteen trials. A trial score was only used if the goanna was moving in a straight line past two points whose

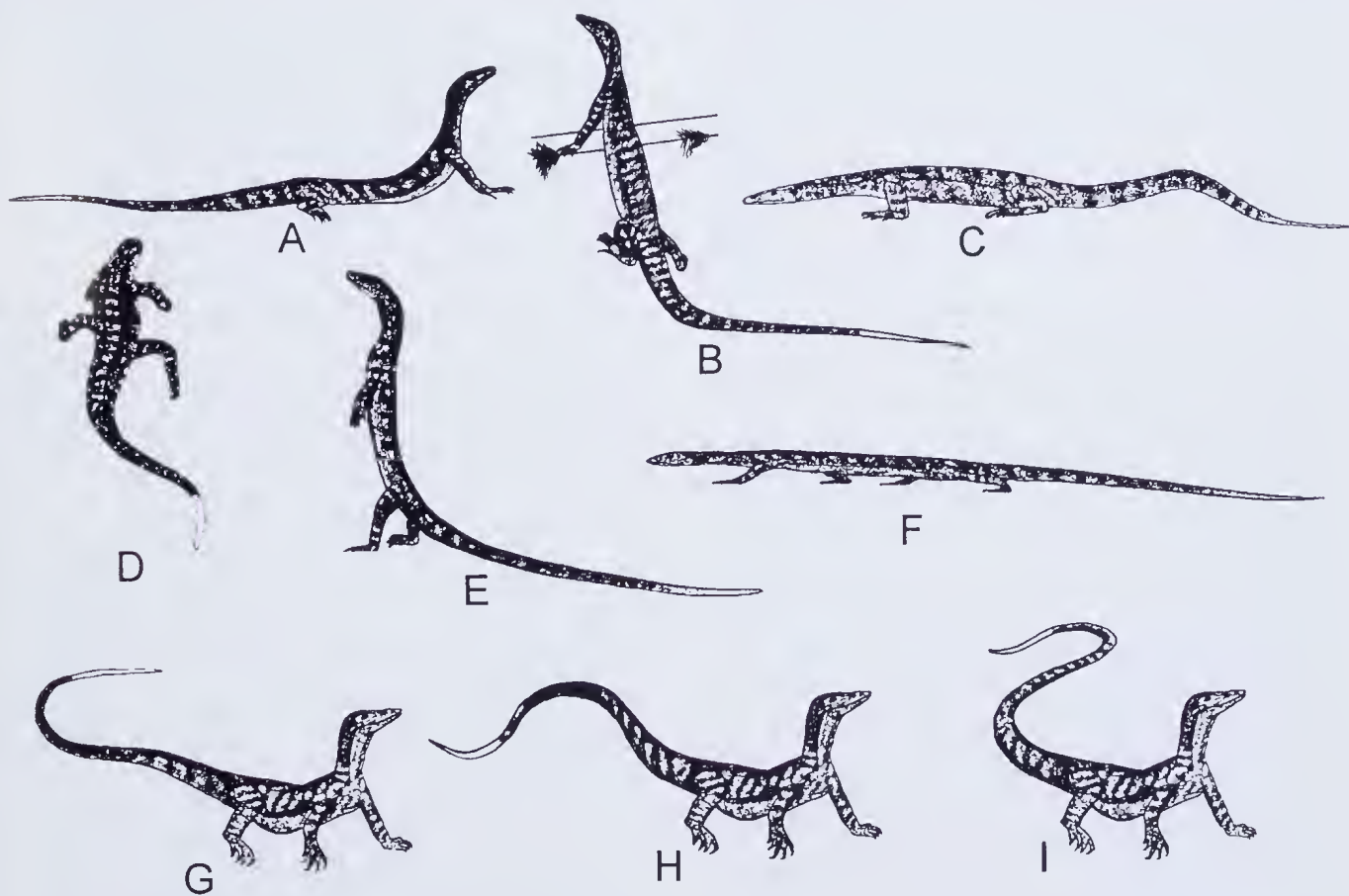


Figure 2. Body postures adopted by *V. gouldii* at Karrakatta Cemetery. A: lying on a grave cover with the posterior abdomen flattened onto the grey concrete surface and the head and neck raised; B: on the side of a grave cover with the abdomen dorso-ventrally flattened and directed towards the sun; C: cloaca and anterior proportion of the tail being wiped on the ground after extruding a scat; D: lateral sigmoidal trotting action shown while walking; E: standing erect by balancing on the hind feet and tail; F: walking with only the distant end of the tail dragging on the ground; G, H, & I: tail swipes with non-aggressive posture.

distance apart could be measured, it did not stop to forage or view the surrounds, had not been obviously disturbed, and was not avoiding being seen or attacked.

The ambient temperature (T_a), one metre above the ground, in the shade of a tree, was recorded every nine minutes, for the duration of the study using a Data-flow logger and a calibrated temperature sensitive probe attached to a transmitter. Occasional measurements of the temperature in the shade about one metre above the ground, surface soil in full sunlight, under a grave cover and on top of a grave cover in the sun were recorded to examine the range of thermal environments available to a goanna at any one time.

Results and Discussion

Emergence and responses to ambient temperature

The goannas were seen to emerge from their over-night retreat on eight occasions between 0700 hours and 0945 hours. The mean T_a on emerging was 23.4 ($\pm$ se 0.98) °C. On 15 occasions, the *V. gouldii* had emerged unseen before 0900 hours, and on another 11 occasions the goannas had not emerged by 0945 hours. As has been reported for other varanids (Sokolov *et al.* 1975; King 1980; Weavers 1983), these two goannas would most often poke their heads out of their burrows for a while before their whole bodies emerged in the sun, suggesting that they are initially warming their heads possibly to increase the functioning of their nervous system (King & Green, 1993a). Once the *V. gouldii* had moved from under the grave cover and onto the top of it, they would dorso-ventrally flatten and lower their abdomen onto the grave cover so as to expose the greatest body surface area for both radiative and conductive heat gains (Fig 2A). They would remain constantly vigilant during this period (2 - 35 minutes) with head and neck held aloft, until they moved off to forage.

After emerging and basking, foraging most often commenced in an area of full sunlight, and the goannas would often seek partially-shaded or fully-shaded areas to forage as the ambient temperature increased. A mean ambient temperature of 25.8 °C ($\pm$ se 0.75, $n = 14$) was recorded for the first nine minute period that the goanna spent in either in $\frac{3}{4}$ shade or a full shade. *V. komodoensis* are reported to adopted a similar strategy of moving from sunny areas into the shade as the ambient temperature increases (Auffenberg 1981a). One *V. gouldii* (#1), while vigorously digging out a spider's hole in full sun-light (ambient T_a of 27.3 °C, 10:30 hours), stopped on three occasions to open its mouth to gular pant. When it finally had caught the spider, it moved quickly to the closest shade. The gular panting by *V. gouldii* in this situation was probably an indication that the goanna was approaching its critical maximum T_b in response to solar radiative heat gain and perhaps metabolic heat production from the vigorous activity. Hyoid breathing (or gular panting) occurs at a T_b of approximately 39 °C for *V. rosenbergi* (King 1977, p.126) and 41 °C for *V. griseus* (Vernet *et al.* 1988b). Auffenberg (1981a) reports that gular panting indicates that *V. komodoensis* is approaching its critical maximum T_b .

Measurements of the temperature in the shade about one metre above the ground, surface soil in full sun-

light, under a grave cover and on top of a grave cover in the sun were occasionally recorded to examine the range of thermal environments available to a goanna at any one time. After mid-morning when the surface soil and grave covers had heated up, a wide variation in thermal environments were most often recorded (e.g. on December 24 at 1015 hours, air temperature was 27 °C, under grave cover temperature was 24.1 °C, surface soil temperature was 39.6 °C and on top of a grave cover it as 46.4 °C) enabling the goanna to effectively regulate its body temperature by choosing a particular thermal environment.

Foraging site selection

The general habitats and foraging micro-habitats selected by the two goannas were determined for periods of 41.05 and 26.55 hours respectively (Table 2). The activity area for each goanna (Fig 1) was determined by the smallest convex polygon that incorporated all of the locations that each lizard was found. The activity area of *V. gouldii* #1 (7.8 ha, excluding the bitumen road and the area outside the cemetery boundary) was approximately 61% open ground with almost no leaf litter, 16% tree canopy with a ground cover of leaves, 10% grassed area, 11% leaf litter on open ground, and 2% shrubs with a leaf litter ground cover (grave covers were included in the total space calculations according to the immediate surrounds). The activity area of *V. gouldii* #2 (8.5 ha) was 42% open ground with almost no leaf litter, 34% grassed area, 7% a tree canopy and ground cover of leaves, 12% leaf litter on open ground and 5% shrubs with a ground cover of leaves (Fig 1). The activity areas for these two goannas were substantially larger than were recorded for six other female *V. gouldii* ($2.29 \pm$ se 0.23 ha, range 1.6 - 3.28 ha, mean mass = 380 g) measured during the previous breeding season (Thompson, 1994). It is not known if there was a real difference in activity area sizes, or whether the presence of an

Table 2. The percentage of time spent by two *V. gouldii* range of habitat types and selected microhabitat foraging sites. The data reported comes from 65 hours of observations and only includes the time between when *V. gouldii* commenced foraging until the goannas either returned to a burrow or observations ceased.

Habitat type	Percentage of time	
	<i>V. gouldii</i> #1	<i>V. gouldii</i> #2
Between graves	35.6	39.7
On top or the side of graves	27.5	35.0
Under grave covers	12.2	9.9
Grassed areas	9.9	5.5
On the road verge	4.8	4.2
Treed areas	3.6	4.7
In yards of adjacent houses	3.2	0.0
In nature reserve	3.1	0.0
Up a tree	0.0	1.0
Micro-habitat foraging sites within activity area		
Between grave covers	47.7	77.9
Leaves under trees or shrubs	19.7	9.9
Under grave covers	13.7	4.2
Leaves in an open area	9.8	5.6
Grass in an open area	8.1	2.4
Grass under trees or shrubs	0.9	0.0

observer increased the size of these activity areas, or the difference was due to the different nature of the data used to calculate the activity areas. In the earlier study, only one location was recorded for each goanna each day, and the total activity area was calculated from the smallest convex polygon that included all recorded locations. In this study, the location of each goanna was known for up to half a day over a period of approximately six weeks. Continuous observations are more likely to determine the real boundary of a goanna's activity area than would single daily observations, a factor not taken into account by the 'direct' polygon method used by Thompson (1994). Perhaps a better comparison might be with the activity area sizes calculated using the Jennrich & Turner (1969; females mean activity area of 3.91 ha $\pm$ se 0.36) approach, or the weighted ellipse (Samuel & Garton 1985; females mean activity area of 3.1 ha $\pm$ se 0.33).

Both goannas spent the highest proportion of their foraging time (47.7% for #1 and 77.9% for #2) in the leaf litter between grave covers, without a tree or shrub canopy. These areas were estimated to be only 11 and 12% respectively of their total activity areas (Fig 1). The leaf litter between grave covers had often accumulated to a depth greater than 50 mm and many of the grave covers contained a hole under the edge, into which the goanna could retreat. It could be speculated that these two goannas selectively chose these area to forage because the leaf litter provided a good food source (Marginal Value Theorem; Charnov 1976) and the grave covers were suitable protection from predators. The two other most-foraged habitats were the leaf litter under trees and shrubs (#1, 19.7% and #2, 9.9%), and under grave covers (#1, 13.7% and #2, 4.2%). Trees and shrubs with a ground cover of leaf litter under the canopy comprised approximately 18 and 12% respectively of the activity areas of these two goannas. The shrubs and trees provided both shade in the hotter parts of the day, which enable the varanids to continuing foraging within their ecritic body temperature range, camouflage protection and a source of food in the leaves.

On one occasion, *V. gouldii* #2 climbed up in to a shrub that was approximately 1500 mm high and wide, and was observed to search the foliage, for a period of over 23 minutes. During this time, it climbed onto and searched almost every branch in the shrub that would support its body mass. Pianka (1970) reported that *V. gouldii* sought refuge in trees, but Thompson & Homer (1963) suggest that *V. g. flavirufus* was not arboreal. Thompson (1994) reports finding four *V. gouldii* up trees in Karrakatta Cemetery with 'no evidence to suggest that they had been chased into this situation'. He speculated that they might have been thermoregulating or foraging. In this study, the arboreal *V. gouldii* was actively foraging.

Foraging patterns and behaviours

V. gouldii #1 was seen to catch 64 prey items (spiders, insects and skinks) during a period of 35.5 hours of observation over 17 days. This was equal to one prey item being captured every 33.3 minutes. One scat was normally produced by each goanna each morning within an hour of commencing to forage. At the completion of excreting the scat, the *V. gouldii* would

raise the middle and distal end of its tail, and drag its cloaca and the proximal end of the tail on the ground for 8-12 cm (Fig 2C).

The two *V. gouldii* appeared to use both visual and auditory cues to detect their prey from a distance. When a goanna approached a patch of leaves, it would slow its forward speed of movement, move its head and neck slowly from side-to-side, using the snout to shift leaf litter while flicking the tongue in and out. The front feet were often used to scratch leaves away or dig into the ground for prey items. The use of the flicking forked tongue was taken as an indication that the lizard was using olfactory cues to find prey (Pianka 1982; Auffenberg 1984; Cooper 1989; Garrett & Card 1993). Once a prey item had been located, the *V. gouldii* would normally persist searching until the prey was captured, or in excess of five minutes. On one occasion, *V. gouldii* #2 was monitored while foraging in an exposed location (full sun-light), on a grassed area adjacent to a water pipe; having detected a prey item, it searched a small area for over 20 minutes before catching a small skink, then quickly moved to a shaded and more protected area. *V. gouldii* #1, on two occasions, was observed to jump approximately 300 mm into the air to try to catch an insect flying over its head; on both occasions it was unsuccessful.

On five occasions, *V. gouldii* were observed to dig a triangular shaped hole, with the apex adjacent to a spider hole, to excavate the spider. The goanna used its front feet to dig the sand from the hole and the back feet to remove the small pile of sand that accumulated at the top of the hole. The back feet were never observed to assist in digging the hole itself. All prey that were caught were quickly oriented in the mouth and swallowed, without signs of chewing. The goanna would often wipe the sides of their jaws on the ground after swallowing their prey.

Influence of birds on foraging sites

The foraging of these two *V. gouldii* at Karrakatta Cemetery was influenced by the rainbow bee-eater (*Merops ornatus*) and the red wattlebird (*Anthochaera carunculata*). A bee-eater was seen to swoop on a *V. gouldii* on 13 different occasions, and chase it away from their nesting holes (into the soft sand areas of the cemetery). The goanna would lower its head during the final moments of such an attack, to avoid contact, and would quickly retreat to a more secure location. Bee-eaters were observed to actually contact a goanna on five occasions. On one occasion, the goanna ran approximately 70 m after being harassed to find protection under a grave cover. The red wattlebird was also observed to swoop on a goanna on 12 occasions; contact with the lizard's head was seen on one occasion. It appeared that goannas had learnt to distinguish the particular calls of the red wattlebird and the rainbow bee-eater from other noises, as they would adopt a vigilant posture upon hearing their calls and move away from the direction of the call or under a shrub or tree to avoid being swooped on. Poiani (1991) reports another wattlebird (*Manorina melanophrys*) responding to the presence of *V. gouldii* with an alarm call.

Movement speeds and distance travelled while foraging

Little is known of the speed at which varanids forage, although the total distance moved in a given period is known for a number of large varanids. For example, Stebbins & Barwick (1968) report a 4.2 kg *V. varius* to travel a total distance of 2.9 km over a five day period in November, and Weavers (1993) reports the same species to travel up to 1.63 km day⁻¹ in south-eastern New South Wales. Vernet *et al.* (1988b) report *V. griseus* in the north-western Sahara desert to cover between 0.1 and 2.5 km day⁻¹; Pianka (1970, 1971, 1982) reports following *V. gouldii* for 'over a mile', *V. tristis* for 'nearly a mile' and *V. eremius* for 'up to a kilometre' in a day, in semi-arid environments of Western Australia. Auffenberg (1981a) reports the much larger *V. komodoensis* to travel as much as 10 km day⁻¹, with a mean of 1.8 km day⁻¹, while Alberts (1994) reports *V. albigularis* in Namibia to travel as much as 4 km day⁻¹ during the mating season. *V. gouldii*, with a body mass of less than 600 g (measured in a previous year during October and November) travelled an appreciably shorter distance per day (mean 158 m day⁻¹; Thompson 1992). In this study of two *V. gouldii*, the average speed was 2.6 m min⁻¹ while foraging; *V. gouldii* #1 covered an estimated total distance of 7010 m in 42 hours of activity time (a mean speed of movement of 2.78 m min⁻¹), while *V. gouldii* #2 covered an estimated total distance of 2238 m in 23.5 hours of activity time (a mean speed of movement of 1.59 m min⁻¹). The speed of movement between foraging patches was considerably higher, at 27.6 m min⁻¹ (se = 1.92, range of 18.6 to 40.2 m min⁻¹), which was about ten times the overall mean speed of foraging. Goannas seldom moved in a straight line when moving between foraging sites and when foraging. Therefore, the mean speed of movement between foraging patches and the mean speed of movement while foraging are probably underestimates because the actual distance covered in each trial was greater than the linear distance recorded. However, the underestimation is probably quite small, because most of the movement by the two goannas occurred between grave covers where circuitous movements are constrained by the walls of the graves. Trials to establish movement speed between foraging sites were conducted adjacent to grave covers of known dimensions.

Body postures

V. gouldii frequently stopped during foraging to adopt a 'vigilant' posture. This posture was characterised by the body remaining motionless, the abdomen held in either a prone or erect position, and the head and neck held high. The goanna would slowly rotate its head a couple of times to give a clear view of the surrounding area, while the posterior part of the abdomen and tail rested on the substrate. When a grave cover was nearby, the goanna would sometimes climb onto the side (Fig 2B) or top of the grave cover during foraging, adopt this vigilant posture, then return to the ground to continue to forage. On a few occasions, a goanna was observed to stand erect, by balancing on the hind legs and tail (Fig 2E). This stance appeared to be prompted by the need to see over some obstruction, as it occurred when the *V. gouldii* were between graves and their vision of the surrounding area was obstructed. A similar erect posture has been reported by Glazebrook

(1977) for *V. gouldii* standing erect on its hind legs to obtain a better view of its surrounding. Auffenberg (1981a) reports adult *V. komodoensis* standing erect to take food suspended in the air, and young *V. komodoensis* standing erect to look over tall grass. King & Green (1993a) show a *V. panoptes* in a similar upright stance. These erect stances are different from the bipedal threat displays of *V. mertensi* (Murphy & Lamoreaux 1978), *V. panoptes* (King & Green 1993b, p257; Wilson & Knowles 1992, p318; Bennett 1992), *V. gouldii* (Grigg *et al.* 1985, p vii; Horn 1985) and for several other species (Beste & Beste 1977, p89) where the neck is arched, the gular pouch extended and the goanna hisses while rapidly flicking its tongue in and out. The aggressive body postures reported by King & Green (1993a, b) for varanids generally, Auffenberg (1981a) for *V. komodoensis*, Bennett (1992) for *V. panoptes*, Stanner (1985) for *V. griseus*, Johnson (1976), Murphy & Lamoreaux (1978) for *V. mertensi*, Pianka (1970) and Stirling (1912) for *V. gouldii*, and Daltry (1991) for *V. salvator* were not seen for the *V. gouldii* at Karrakatta Cemetery. Rather, these goannas appeared to adopt an avoidance behaviour when threatened.

Tail swipes (4 and 8 in quick succession) were observed on two occasions. On neither occasion were they associated with an inflated gular pouch and abdomen, or a hissing sound, as reported by King & Green (1993a) to represent an aggressive stance. On the first occasion, *V. gouldii* #1 approached to within a couple of metres of the observer, raised and turned its head slightly to the side and moved its tail from side-to-side four times (Fig 2G, H and I). On the second occasion, *V. gouldii* #2 was digging for prey. I have observed a similar 'tail-swipes' behaviour for a male *V. gilleni* courting a female of the same species. Additional observations are necessary before this behaviour can be accurately interpreted.

V. gouldii are primarily quadrupedal and terrestrial. After they had emerged from their overnight burrow, elevated their T_b, and commenced moving around their foraging site, they were observed to 'drag' a substantial proportion of their tail on the ground. As the morning progressed, the tail was often lifted off the ground, or only the distal 20% was dragged on the ground (Fig 2F). A lateral sigmoidal trotting (diagonally opposite feet advancing together) while walking was often evident (Fig 2D). The head was normally swung slowly from side-to-side, and at the same level as the body (Fig 2F). The walking posture of *V. gouldii* was therefore similar to that described by King & Green (1993a) for varanids generally, and by Auffenberg (1981a) for *V. komodoensis*, except that *V. gouldii* would sometimes lift their tail off the ground while walking and not leave a tail drag mark. The dorsal surfaces of the rear toes were often dragged along the ground extending the length of their spoor, similar to that reported for *V. komodoensis* (Padian & Olsen 1984).

On twelve occasions, *V. gouldii* #1 was observed, while stationary, to raise its tail so that the distal end was vertical. The same tail raising posture was not observed for goanna #2. A similar stance has been reported for *V. tristis* (Christian 1981); its long tail was curled in a long arc so that the tip would almost touch the back of the neck. The role of this body stance is unknown.

Detection by a goanna of a person, dog or other source of potential danger resulted in one of two initial responses. The goanna would either flatten its body on the ground and remain motionless until the source of danger had passed, or it would slowly move behind a nearby object and would remain motionless. Some two to ten minutes later, it would poke its head around the object to determine if the danger had passed. Alternatively, if the goanna had just emerged from a burrow or a burrow was nearby, it would return to this burrow instead of hiding behind an object. *V. gouldii* appeared to run to a burrow only if the source of danger came very close.

Acknowledgements: Funding for this project was provided by Edith Cowan University. Constructive review of early drafts of the manuscript by P C Withers, M Bull and D King were most appreciated as they improved the final manuscript. The field assistance of S and W Thompson in undertaking most of the observational study was very much appreciated. Access to the Karrakatta Cemetery was approved by the Metropolitan Cemeteries Board, and the assistance of cemetery staff is acknowledged. All goannas were caught under licence issued by the Department of Conservation and Land Management. Animal experimentation was done with the approval of the Animal Welfare Committee of Edith Cowan University.

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THE ROYAL SOCIETY OF WESTERN AUSTRALIA INCORPORATED

Constitution and Rules and Regulations

(Revised March 1996)

Constitution

1. The scientific society known as "The Royal Society of Western Australia Incorporated" (hereinafter referred to as "The Society") has the objects, purposes, and powers hereinafter mentioned.

Objects, purposes, and powers
2. To promote and assist in the advancement of science.
3. To print and publish, or join in printing and publishing, one or more journals, periodicals, books, newsletters or other documents relating to science.
4. To promote, produce and to hold, or join in promoting, producing and holding meetings, lectures, conferences, symposia, excursions and exhibitions in furtherance of any objects of The Society.
5. To found, subsidise or contribute to, for the benefit of any institutions or persons, scholarships, grants, prizes, or monetary or other rewards in connection with all or any of the objects or purposes of The Society.
6. To acquire by purchase, lease, exchange, hire, or by way of loan or otherwise, any real or personal property in furtherance of any objects of The Society.
7. To invest, sell, lease, hire, mortgage, charge, lend, surrender or otherwise dispose of, or deal with all or any part of the assets or property, real or personal, of The Society, or to borrow money and grant security therefore and to liquidate, redeem or discharge any obligations undertaken in furtherance of any objects of The Society.
8. To improve, develop or extend all or any of the property or rights of The Society, also to build, erect or alter any buildings or erections, and to furnish, fit up, and maintain the same and provide fittings, equipment and appliances.
9. To amalgamate, co-operate or affiliate with any other society, association or body having objects wholly or in part similar to those of this Society.
10. To protect or assist in protecting the interests or rights of any member or members of The Society.

Rules and Regulations

Membership

11. The Society shall consist of members who are all individuals involved, assisting or interested in the promotion and/or advancement of science. Members shall be divided into the classes hereinafter mentioned, and the members who are, have been, or may be duly elected as members of such respective classes shall have the rights and privileges hereinafter specified as appertaining to such respective classes, subject always to the due and punctual payment of the annual subscription or other sum hereinafter provided to be paid by the respective members of each class, namely:
 - (a) Ordinary Members: An Ordinary Member if financial shall have the following rights and privileges:
 - (i) To be present and to speak and vote at Ordinary, Special or Annual General Meetings of The Society, to vote in postal ballots conducted by The Society, and to attend excursions, meetings, lectures or other activities arranged from time to time by The Society.
 - (ii) To be eligible for election as a member of the Council hereinafter referred to and also to any office or position in The Society.
 - (iii) To submit to the Council for consideration for publication papers prepared on any scientific subject.
 - (iv) To receive the Journal of The Society.
 - (v) To receive other publications or documents issued by The Society, upon such conditions as the Council may from time to time determine.
 - (vi) To borrow books, periodicals, papers, or other documents belonging to The Society, subject to the approval of the Council.
 - (vii) To propose or second candidates for admission as Ordinary, Associate or Student Members of The Society.
 - (viii) At any meeting held by The Society to introduce visitors. Such visitors shall not be

entitled to vote at any such meeting or excursion, but may express opinions on any matter under discussion at the invitation of the chairman or leader.

- (ix) To propose or second any Honorary or financial Ordinary Member for election to the Council.
 - (b) Associate Members: Persons elected as Associate Members shall be entitled to attend and speak at general meetings, excursions and other activities conducted by The Society, but shall not be entitled to vote at any meeting, and if any such member should vote, then that vote shall not be counted. Associate Members shall be entitled to submit papers for publication, but shall not receive the Journal of the Society except at a price fixed by the Council from time to time and subject to the approval of the Council, may borrow books, periodicals or other documents belonging to The Society, but shall not be entitled to be proposed for, or elected to, any office in The Society, nor to propose or second others for membership or office in The Society.
 - (c) Student Members: The Council may, on application to be made each year in such form it may require, admit as Student Members, persons who are undertaking full-time studies in Western Australia, or as agreed by Council. Student Members shall have the same rights and privileges, and shall be subject to the same restrictions, as Associate Members, except that they shall receive the Journal of the Society.
 - (d) Honorary Members: The Society at its Annual General Meeting in any year may, on the recommendation of the Council, admit as Honorary Members persons distinguished in Science or as patrons thereof, but only in so far as the number of such members shall not henceforth at any time exceed five percent of the total Ordinary, Associate and Student membership of the Society. Honorary Members shall have the same rights and privileges as Ordinary Members, but without liability for any subscription.
 - (e) Honorary Associate Members: The Society at its Annual General Meeting in any year may, on the recommendation of the Council, admit as Honorary Associate Members persons interested in science, but only in so far as the number of such members shall not exceed five percent of the total Ordinary, Associate and Student membership of the Society. Honorary Associate Members shall have the same rights and privileges, and be subject to the same restrictions, as Associate Members, but without liability for any subscription.
 - (f) Corporate Members: Corporate membership may be made available by the Council to organisations under such terms and with such rights and privileges as the Council may determine.
12. Every person desirous of becoming an Ordinary or Associate Member of The Society shall make

application in the form prescribed from time to time by the Council and shall be proposed by an Ordinary or Honorary Member of The Society and be seconded by at least two other Ordinary or Honorary Members of The Society, to each of whom the applicant is known personally. Each application shall be accompanied by the subscription applicable to the class of membership sought and shall be lodged with one of the Secretaries. Each Ordinary and Honorary Member of The Society shall be informed of the application forthwith by such means as the Council may from time to time determine. The Council shall accept or reject each candidate at a meeting of the Council held not less than one month and not more than six months after issue of advice of the candidate's application to the Ordinary and Honorary Members. Admission shall be made by a two thirds majority of those Council members present and voting.

- 13. The Secretary shall inform each candidate of his admission or non-admission to the class of membership sought. Upon admission, Ordinary or Associate Members shall receive a copy of The Society's Constitution and Rules and Regulations. Their membership shall be deemed to apply to the whole of the financial year in which they were admitted so that, subject to their availability, they shall be entitled to receive all publications and documents issued during that year to all members of their class.
- 14. Members of The Society, of whatever class, shall be bound to observe and perform, and not commit any breach of, the Rules and Regulations of The Society from time to time in force.
- 15. Members shall notify the Secretary in writing of their address for receiving notices or communications to be forwarded to them, and shall from time to time notify in writing any change in such address. If any member shall fail to give such notification they shall have no claim against The Society for publications or notices of the meetings or other activities of The Society; notification is deemed to have occurred at the time of posting.
- 16. Members, on paying to The Society all subscriptions or moneys owed by them and returning all books, papers, manuscripts, or property of The Society which they may have borrowed or received, may resign their membership by giving notice in writing to the Secretary of The Society; and any members ceasing by resignation, death, or otherwise to be a member of The Society shall not, nor shall their representatives have any claim upon or interest in the funds or property of The Society; but nothing herein contained shall prejudice the right of The Society to recover any moneys owing or property of The Society borrowed, held, or received by members at any time.
- 17. Members whose subscription may be in arrears for a period of more than two years shall, on a resolution of the Council being at any time thereafter passed, be declared to be no longer members and thereupon shall cease to have the rights and privileges to which they may have been entitled, provided always that nothing herein contained shall

prejudice the right of The Society to recover from such members all moneys or subscriptions due, owing, or payable by them up to the date of such termination of their membership, and also to recover all books, papers, manuscripts or property belonging to The Society which may be held or have been received by such members at any time.

18. Members in the respective classes of membership in The Society shall use their best efforts to promote the objects of The Society and shall not do or commit any act, deed, or thing which may be deemed by the Council to be prejudicial to the interests of The Society.
19. The Council may, by an affirmative vote of two thirds of its total membership, remove or suspend from membership or expel any member of The Society. Notice of such removal, suspension, or expulsion, shall be sent by registered post to the last known address of the member concerned within seven days after the decision of the Council. Members against whom such decision of removal, suspension, or expulsion shall be made, shall be entitled to appeal to a Special General Meeting of The Society by notice to be forwarded by them in writing, addressed to the Secretary within two months after the date of such removal, suspension, or expulsion, stating in such notice the grounds of appeal. It shall be the duty of the Council to summon a Special General Meeting of The Society for the purpose of considering any such appeal, and of hearing statements by any Member of the Council or by the member who may have been removed, suspended or expelled, and if a majority of the members present at such meeting uphold the decision of the Council, then the decision of the Council shall be confirmed, but if such majority shall uphold the appeal, then the decision to remove, suspend, or expel such member shall be set aside. No members shall be entitled to exercise such right of appeal after the expiration of the said period of two months. In the event of any such removal, suspension, or expulsion taking effect, any members concerned shall remain liable for all moneys or subscriptions due or payable by them as at the date of such removal, suspension, or expulsion, and for the return of all property belonging to The Society.

Subscriptions

20. The subscription for each ordinary membership shall be set from time to time on recommendation of the Council and approval by a resolution passed by a two-thirds majority of Ordinary Members voting at any Ordinary or Annual General Meeting of The Society, of which at least twenty eight days notice has been given, and in which notice the proposed alterations have been specified.

Ordinary Members whose subscriptions are not in arrears shall be granted Ordinary Membership for Life upon payment of a fee of twenty years subscription at the rate of the current year.

21. Associate Membership shall not be more than 60 percent of the Ordinary Membership rate.

22. Student Membership shall not be more than 60 percent of the Ordinary Membership rate.
23. The financial year of The Society shall be from the first day of July in each year to the thirtieth day of June in the following year.
24. All subscriptions shall be payable in advance and shall become due on the first day of July in each year. Any member whose subscription is unpaid six months after the due date in any year shall be deemed to be not financial. After this date a late fee shall be payable at a rate determined by Council from time to time.

Management

25. The management of the business and affairs of The Society shall be vested in a Council consisting of a President, two Vice-Presidents, Treasurer, three Secretaries, Librarian, Editor, Journal Manager, Immediate Past President and seven Ordinary or Honorary Members of The Society.
26. All members of the Council shall be elected at the Annual General Meeting of The Society to be held on a date normally in July at a place to be decided by the Council and serve for a term of one or two years. For the purpose of such election the Council then in office shall submit, at an Ordinary or Special General Meeting held not less than one calendar month before the Annual General Meeting, a list of names of Honorary or financial Ordinary Members proposed by the Council for election indicating the length of term of office and shall appoint a Returning Officer. Any Ordinary or Honorary Member present at such Ordinary General Meeting shall be entitled to propose another financial Ordinary or any Honorary Member to hold any position on the Council, and if such nomination be duly seconded and if the candidate nominated has signified willingness to accept office if elected, then the name of such nominee shall be added as a candidate. Further, any Ordinary or Honorary Member of The Society may lodge with the Returning Officer within seven days after that Ordinary or Special General Meeting, preceding the Annual General Meeting, a nomination in writing in favour of any financial Ordinary or any Honorary Member for any position on the Council. Such written nomination shall be seconded by another Ordinary or Honorary Member, and shall carry a statement by the candidate nominated as to their willingness to accept the office if elected. Upon receipt of such nomination, the Returning Officer shall add the name of the nominee as a candidate for the Council.
27. If the number of members duly proposed for election does not exceed the number of vacancies for the various offices, the Chairman of the Annual General Meeting shall declare the persons nominated as duly elected. If the number of nominations for any office exceeds the number of vacancies, an election shall be held and the results ascertained by preferential ballot. For the purpose of such election, a ballot paper containing the names of all persons duly proposed for all contested positions on the Council

shall be prepared by the Returning Officer and sent to all Ordinary and Honorary Members. Such members desirous of voting shall cause to be delivered to the Returning Officer such ballot papers, duly completed in accordance with any instructions on voting procedure before the formal opening of the Annual General Meeting. The Annual General Meeting shall appoint at least two scrutineers, who shall examine the procedures of the Returning Officer in the counting of votes and who shall report the results of the count to the Chairman of the Annual General Meeting. Such Chairman shall announce the result of the ballot at the Annual General Meeting or at the next Ordinary or Special General Meeting of The Society.

28. All members of the Council shall be eligible for re-election.
29. Any casual vacancy in the Council may be filled by resolution of the Council, and any member so appointed shall hold office until the next annual election of Council. Any vacancy not filled at the annual election shall be deemed a casual vacancy.
30. The Council may define the duties of the three Secretaries and may add any distinguishing word to the title of any or all Secretaries in accordance with the nature of the duties to be performed.
31. The Council shall meet at least once in each month from February to November inclusive in each year (unless otherwise decided by Council), at such times and places as may be appointed by the President, or in the President's absence, by one of the Vice-Presidents, and due and sufficient notice shall be previously sent to each member of the Council.
32. A quorum for a meeting of the Council shall be the President or one of the Vice-Presidents, a Secretary who may be specially appointed for that meeting, and four other members of the Council, and no business shall be transacted at any Council meeting unless such quorum is present.
33. If any members of the Council (including holders of offices) shall fail to attend three consecutive meetings of the Council without satisfactory explanation or reason, or without leave of absence having been first granted to them, then the position or office of such member may by resolution of the Council be declared vacant, and on passing of such resolution they shall cease to be a member of Council and holder of any office to which they may have been elected.
34. Council shall inform members of activities of the Society including deliberations of the Council by publishing and distributing to the members a Proceedings following each Ordinary or Annual General Meeting.
35. The Council shall present at each Annual General Meeting a report giving a review of the work of The Society during the preceding year and some details and information with regard to its progress and affairs, and shall publish this report.
36. The Council may appoint a Committee from among the financial members of the Society, and by two

thirds majority resolution may include non-members in such a Committee. A Committee may be of such number as the Council may decide and may consider and make recommendations on any subject on which Council may require advice, provided that such a Committee includes at least one Council Member. Each Committee so appointed shall be reviewed at regular intervals to be determined by the Council.

37. The Council may from time to time make, alter, and repeal by-laws to enable it more effectually to carry out the management of the affairs of The Society, and to regulate the conduct of members and assist in the protection of its property, and for such purposes as may be calculated to advance the welfare of the Society, provided that such changes are not inconsistent with these Rules and Regulations.
38. The Council, without limiting its general powers of management and carrying on the business and affairs of The Society, may exercise and do all things necessary except such as may be required or directed to be exercised by General Meetings, including power to appoint and remove all or any officers, assistants, employees, or others deemed by the Council to be necessary in connection with the work of The Society, and that with or without remuneration and upon such terms and conditions as the Council may think fit. The Council may also delegate all or any of its powers or authorities to any committee or sub-committee from time to time, and may pay all or any expenses or liabilities incurred from time to time and take any steps or proceedings which may be deemed desirable for the purpose of carrying out or securing the fulfilment of any of the objects or purposes of The Society.

President and Vice-Presidents

39. The duties of the President shall be to preside at all meetings of The Society and Council, and regulate all the proceedings therein and generally to execute or see to the execution of the Rules and Regulations and by-laws of The Society. In the case of an equality of votes at any meeting, the President or Vice-President or member presiding shall have a casting vote in addition to a deliberative vote.
40. In the absence of the President from any meeting of the Council, the President's place shall be filled by one of the Vice-Presidents. In the absence of the President from any other meeting or excursion of The Society, the President's place shall be filled by one of the Vice-Presidents or by an Ordinary or Honorary Member of The Society elected as Chairman or leader by the Ordinary and Honorary Members there present.

Duties of Officers

41. The Secretaries shall conduct correspondence, arrange meetings, cause notices of meetings and Proceedings to be sent out, keep adequate records of all meetings, membership and other activities of The Society, and generally perform such duties as are usually assigned to persons holding such office and

comply with the directions, requests, or instructions issued from time to time by the Council.

42. The Treasurer shall keep a correct record of all receipts and disbursements, including subscriptions and all moneys received for the benefit of The Society, and shall pay those moneys forthwith to the credit of The Society at its bankers. It shall be the duty of the Treasurer to pay all accounts passed by the Council. No moneys shall be withdrawn from the bank account except by cheque signed by any two of a group of three or more members of the Council which shall include the Treasurer and two or more other members of Council so authorized by Council. The Treasurer shall cause the books of The Society to be posted regularly, and shall bring his books to balance as on the thirtieth day of June in each year, or on such other date as the Council may from time to time decide.
43. The Treasurer shall annually submit to an Auditor or Auditors all books and accounts kept by the Treasurer in connection with the affairs of The Society, made up to the date last mentioned. The Society shall, not later than its Ordinary General Meeting immediately prior to the Annual General Meeting, appoint an Auditor or Auditors, but if such Ordinary General Meeting shall fail to make such appointment, then the Council may appoint an Auditor or Auditors.
44. It shall be the duty of the Auditor or Auditors of The Society to submit a written report each year on the financial affairs of The Society through the Council to an Ordinary, Special or Annual General Meeting of The Society.
45. The Librarian shall maintain records and generally manage the books, periodicals and documents of The Society according to the directions of the Council.
46. The Editor shall supervise the production of The Society's Journal and such other publications as the Council may direct.
47. The Journal Manager shall supervise the distribution of The Society's Journal and other publications as authorized by Council.
48. Other members of the Council shall assist in the general management of The Society according to the needs which may arise from time to time.

Ordinary General Meetings

49. Ordinary General Meetings of The Society shall be held at 8 p.m. on the third Monday of the months March to June and August to December inclusive in each year, unless the Council determines otherwise, but at least three Ordinary General Meetings shall be held in each financial year. Notice of each Ordinary General Meeting shall be sent to all members of each class. A quorum for an Ordinary General Meeting shall be seven Ordinary or Honorary Members personally present. Conduct of an Ordinary General Meeting shall be at the discretion of the President or Chairman elected by such meeting.

Annual General Meetings

50. The Annual General Meeting of The Society shall, unless the Council determines otherwise, be held on the third Monday of July in each year at a time and place determined by the Council. Notice of each Annual General Meeting shall be sent to all members of each class at least one calendar month before such meeting.
51. The proceedings of the Annual General Meeting, unless otherwise determined by the Council, shall be as follows:
 - (a) Presentation of the minutes of the previous Annual General Meeting.
 - (b) Reading of nominations of candidates for Council, and, if necessary, appointment of scrutineers, and counting of votes.
 - (c) Presentation of the Annual Report of the Council.
 - (d) Presentation of the Balance Sheet, Statement of Accounts and (if available) Auditor's Report.
 - (e) Report (if necessary) of the scrutineers on the ballot and declaration of the results by the retiring President.
 - (f) Address by the retiring President.
 - (g) Installation of the new President.
 - (h) Any other business of which notice may have been given prior to or agreed during the meeting to be considered.
52. A quorum for transaction of business at an Annual General Meeting shall be seven Ordinary or Honorary Members of The Society personally present.

Special General Meetings

53. Special General Meetings of The Society may be called by the Council whenever it may deem such meeting expedient, or on the requisition of ten Ordinary or Honorary Members made in writing to one of the Secretaries and specifying the purpose for which the meeting is required. Upon receipt of such requisition, that Secretary shall call the meeting within not less than seven days nor more than twenty eight days. Notice of such meeting shall be sent to all members of each class. The meeting shall be chaired by the President or a Vice-President or, in their absence, an Ordinary or Honorary Member elected by the meeting.
54. A quorum for a Special General Meeting of The Society shall be seven Ordinary or Honorary Members personally present.

The Journal of the Society

55. The Society shall publish a Journal at least once a year, in which papers communicated to The Society during or before that year may be printed. The Journal shall be printed in such form as decided by the Council.
56. Every paper intended to be published in the Society's Journal must be sent to the Editor for con-

sideration by Council. The Editor shall Chair a Publications Committee, if such is appointed by Council, to provide assistance and advice to the Editor.

57. The Editor shall seek an expert opinion from any person or persons the Editor may select as referees to judge the suitability of any paper for publication. The Editor shall recommend to the Council whether or not a paper submitted for publication should be accepted for the Society's Journal. A paper of which the Editor is author or co-author shall be edited by a member of Council, so authorised by Council, who is not a co-author of the paper.
58. It shall be the duty of the Council to decide, on the recommendation of the Editor or authorised Council member, whether or not a contribution shall be accepted for publication.
59. Publication in the Society's Journal shall be available to all categories of members.
60. The original copy of every paper accepted for publication by The Society, with its illustrations, shall become the property of The Society, unless the Council decides otherwise. Authors shall not be at liberty to publish elsewhere papers submitted to The Society for publication in its Journal, unless permission for doing so is given by the Council, or unless the Society fails to publish the paper in the Journal of the year in which it is accepted or of the succeeding year, or does not accept the paper for publication.
61. The published price of the Journal shall be fixed by the Council from time to time.
62. Offprints of papers shall be available to authors on such terms as shall be decided from time to time by the Council.

The Medal of the Royal Society of Western Australia

63. A Medal, for which Council will call for nominations through its Proceedings, shall be awarded by the Council every fourth year or at such other times or periods as the Council may from time to time decide for distinguished work in science connected with Western Australia. The Council shall appoint a Medal Committee consisting of five members of the Council to assess the nominations and recommend a recipient of the Medal. The recipient shall, on the awarding of the Medal, be requested to deliver a public address to be known as the Royal Society of Western Australia Medal Lecture.

Formation of Sections

64. Sections may be formed for the purpose of any particular branch of science. Any member of The Society may be enrolled as a member of one or more sections. Each section shall appoint a Chairman and Secretary, with the approval of Council. Sections shall not incur expenditure without first obtaining the approval of the Council. Any communication to a section may be presented subsequently at a general meeting of The Society.

Common Seal

65. The Common Seal of The Society shall be in the custody of the President or one of the Vice-Presidents, and the President or any one Vice-President shall respectively be authorized to use the same, and when required to be affixed to any deed, document, or writing, shall be so affixed and signed by either the President or one of the Vice-Presidents and countersigned by a Secretary of The Society.

Interpretation of the Constitution and Rules and Regulations

66. The Council of The Society shall be the sole authority for the interpretation of the Constitution and of the Rules and Regulations of The Society, and the decisions of the Council on questions of interpretation shall be final and binding on all members.

Alteration of the Constitution and Rules and Regulations

67. The Constitution or the Rules and Regulations or any of them may be amended, altered, enlarged or repealed from time to time by a resolution passed by 75 percent of Ordinary or Honorary Members voting in a postal ballot conducted by the Council. Notice of intention to conduct such a ballot shall be given with notice of an impending Ordinary or Annual or Special General Meeting of The Society and the proposed amendment or amendments shall be presented at that meeting at least one calendar month before the ballot is held.

Non-Profit Organisation

68. The Society is operated as a non-profit organisation. The assets and income of The Society shall be applied solely in furtherance of its above mentioned objects and purposes and no portion shall be distributed directly or indirectly to the members of The Society except as bona fide compensation for services rendered or expenses incurred on behalf of The Society.

Winding up of The Society

69. The Society may be wound up by a resolution to be passed by a four fifths majority of the Ordinary and Honorary Members of The Society present and voting at a Special General Meeting summoned for such purpose, whereof at least twenty eight days notice shall be given. If a resolution to wind up The Society be passed, and there remains, after satisfaction of all The Society's debts and liabilities including the costs, charges and expenses of that winding up, any property whatsoever, the same shall not be paid to or distributed among the members but shall be given or transferred to some other association or associations which are themselves incorporated under the Associations Incorporation Act 1987 and are therefore non-profit organisations, or for charitable purposes, or both, as determined by resolution of the members.

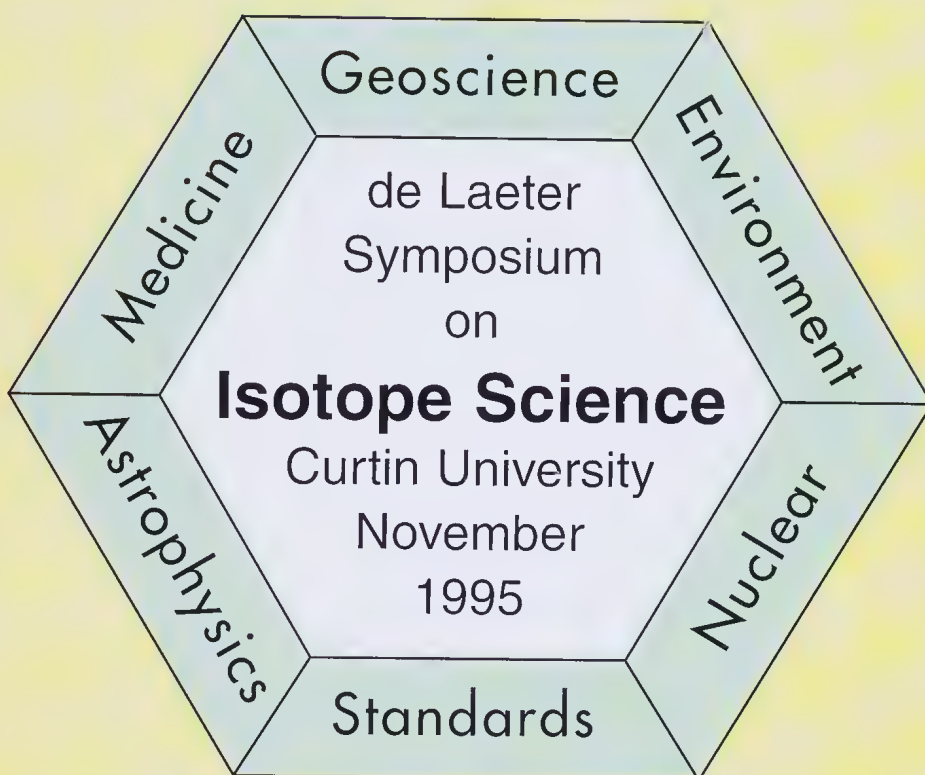


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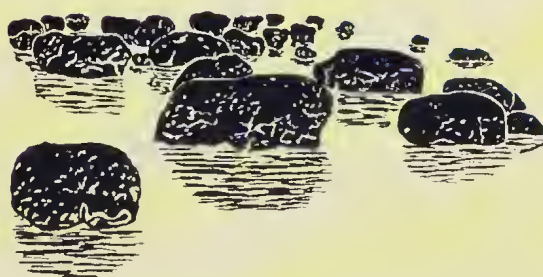


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Volume 79 Part 1
March 1996



Museum of Victoria



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ISSN 0035-922X

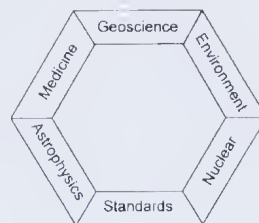


PARTICIPANTS
 de Lacter Symposium on Isotope Science
 6-8 November 1995, Curtin University of Technology, Western Australia.

- FRONT ROW (left to right): Ian McDougall, Bill Compston, Mario Zadnik, Daphne Sands, Sir Marc Oliphant, John de Lacter, Roland Maas, Trevor Ireland, Ross Taylor, Allen Kennedy, David Whitford, Rod Page.
- SECOND ROW: Ian Williams, David Nelson, David Antonjuk, Sarah Gomersall, Bob Loss, Clif Smith, Peter Scherer, Don Rokop, Paul De Bièvre, Lieve De Bièvre, John Moody, G R Carr, Stirling Shaw, Alec Trendall, Ernest Garner, Steve Clement, Bob Pidgeon.
- THIRD ROW: Tom Bowden, Shen-Su Sun, Sue Keay, John Boldeman, Rebecca Sproule, Neal McNaughton, Ken Collerson, Bruno Latella, David Makuyana, Alex Bevan, Ian Fletcher, Ludolf Schultz, Mitsuru Ebihara, Salah Jimi, Kevin Rosman, Jim Delmore.
- FOURTH ROW: Norman Holden, Torbjørn Skjold, Zenon Palacz, Malcolm McCulloch, Brian Gulson, Peter Downes, Peter Kinny, Keith Sircombe, Ron Burman, Steffen Peiser, Ian Nicholls, Janet Hergt, Jon Woodhead, Andrew Walder, James Holmes, Raimier Bryce.



Proceedings of The de Laeter Symposium on Isotope Science¹



edited by

Philip C Withers
and
Kevin J R Rosman

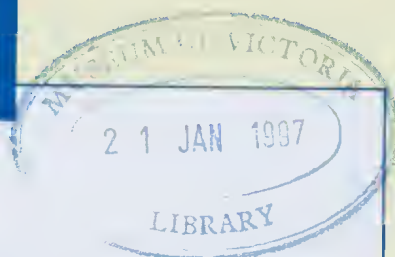
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¹ Held at the Curtin University of Technology, Perth, 6-8 November 1995.



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Volume 79 Part 2
June 1996

Museum of Victoria



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ISSN 0035-922X

The Royal Society of Western Australia



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	V Semeniuk	BSc (Hons) PhD
	L N Thomas	BSc MSc PGDipEIA
	G G Thompson	MEd

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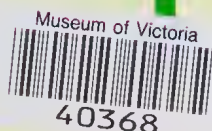
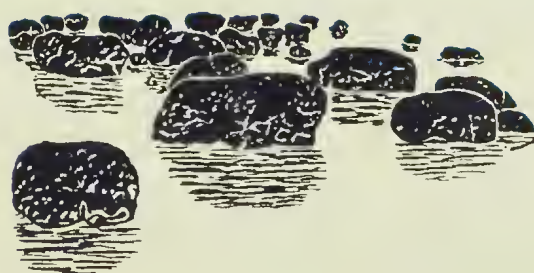


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September 1996



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ISSN 0035-922X

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FOREWORD

The John R de Laeter Special Issue

In 1995, when Professor John de Laeter retired from the post of Deputy Vice-Chancellor (Research and Development) at Curtin University, a unique opportunity arose to combine formal recognition of his broad spectrum of research achievements with an international conference on Isotope Science, the field in which the bulk of his research has taken place. Although initial plans for the conference included Science Education and Science Policy, it was eventually decided that in the two days available we could only do justice to one field.

The de Laeter Symposium on Isotope Science was held on 6-8 November 1995 and attracted 72 delegates from the European Community, the United States of America, Canada, Japan and Australia. Twenty one colleagues and associates journeyed to Perth to contribute papers covering the many areas of Isotope Science to which John has contributed.

The papers in this special issue of the Royal Society's journal are based on these presentations. They span a very wide range of the traditional disciplines and serve to highlight both the interdisciplinary nature of isotope science and the tremendous range of John's interests. The style of the papers is equally diverse: a proportion are current reviews, while others explore the origin and development of important aspects of isotope science. New data and new developments are also presented while other original, but less scientific, contributions also appear.

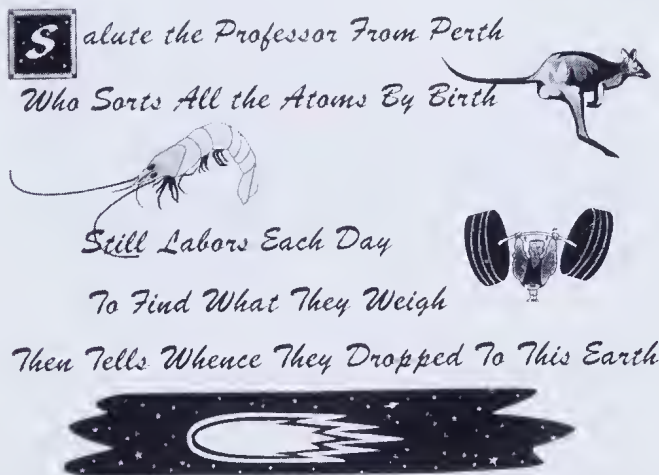
With only minor rearrangement, this volume closely follows the four themes of the Symposium; Measurement Science; Cosmochemistry, Meteorites & Nucleosynthesis; Nuclear & Environmental Science; and Geochronology & Isotope Geology.

The papers are prefaced with an inspiring opening address by Sir Marc Oliphant, who recounts some of his experiences at the Cavendish Laboratory. Sir Marc's participation in the symposium was particularly significant, since a lecture he delivered at the University of Western Australia in 1950 prompted the late Peter M Jeffery to initiate isotope ratio mass spectrometry and geochronology in Australia. Peter Jeffery's infectious enthusiasm for mass spectrometry caught many of us, including John de Laeter.

Overwhelming support for the Conference was received from all parts of Curtin University. Sponsors included The Vice Chancellor's Office, The Division of Engineering and Science, The School of Physical Sciences and The Department of Applied Physics.

Kevin J R Rosman

Convenor of the Organising Committee
for the de Laeter Symposium on Isotope Science
Curtin University of Technology
Perth, WA 6102 Australia



H S Peiser & P R Goodman, 1995
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de Laeter Symposium

In the year 1932, when I was working with Rutherford in the Cavendish Laboratory, Cambridge, he was presented with two drops of almost pure heavy-water by Professor Lewis from Berkeley, California, who had produced them by sustained electrolysis of ordinary water. I separated gaseous deuterium from them, and made stable compounds containing deuterium, by exchange reactions. I then bombarded these salts with positive ions of deuterium. Two products of these reactions were hydrogen and helium isotopes of mass three. Aston was intrigued when I showed him our results, and he then found traces of these isotopes in his mass spectra.

I spoke of our work at a meeting of the Royal Society of London. I was immediately attacked violently by Soddy, who explained that the word isotope was his creation, and a fundamental property of isotopes was that they could not be separated. Rutherford, in the Chair as President, managed to sooth the angry man, but I was terrified!

Aston was still at work in the Cavendish Laboratory at that time. I had attended his lectures, which were straightforward readings of his book, and extremely dull. Aston was the laziest man I ever knew in physics. A bachelor, his hobby was his gramophone, the latest thing in electronics of that time. He was seldom in the Cavendish Laboratory, but when he was he made a great fuss if anyone but he used the storage batteries in the basement, and was still more angry if a spark discharge anywhere produced radiation which upset his mass spectrograph. He was upstairs to me in an instant if I used outgassing equipment during the late afternoon on the rare occasions when he was at work. However, on the whole I got on well with him, though I was unable to persuade him to allow me access to his collection of all the rare gasses stored over mercury!

J J Thomson's lectures on "Electricity in Gases" were good, if one neglected the snapping of his false teeth, which had the habit of falling down every so often. There were stories of his walking all the way from the Cavendish Laboratory in Free School Lane, to Trinity College, of which he was Master, with one foot on the path and the other in the gutter, and complaining that there must be something wrong with his legs! It was clear that he provided the inspiration for Aston's work, and for my own work on the interaction of gaseous positive ions with metal surfaces.

It is grand, therefore, to know that Professor de Laeter has carried further these investigations begun so long ago. I am honoured to open this discussion of his area of work.

Sir Marc Oliphant



John de Laeter and Sir Marc Oliphant (right)

Science to de Laeter: What now comes later

H S Peiser

US National Bureau of Standards (retired), 638 Blossom Drive, Rockville MD 20850 USA

Abstract

Selected episodes of history illustrate developments in science and philosophy by which we try to grasp the realities of immense ranges of scales for time, distances, temperature, mass, and substance. In this epoch of isotope awakening, John de Laeter is a principal contributor, worthy of celebration and institutional pride for Curtin University of Technology. New knowledge and understanding is changing problems and opportunities in physics, chemistry, astronomy, geology, and the biological sciences, including agriculture, the environment and medicine. We can not accurately foresee consequential developments in sciences and technologies. Let our hope rest on reestablishing meaningful communications between science and religions leading to moral codes consistent with modesty in human self perception. Thus alone - but with unforetellable cost from stresses imposed on individuals and societies - we can secure a desirable destiny for humanity.

A salute to John de Laeter and Curtin University of Technology

The de Laeter Symposium is a delightful occasion for celebration. An occasion to praise his achievements, to proclaim the significance of his discoveries, and extol the science in his country. For many of us, overseas visitors, a cordial salute to Australia is very appropriate. Particularly in measurement science, we have recently witnessed this nation's image change from one with dispersed scientific talents to one that houses institutions equal to the foremost centers of scientific excellence.

A trait of Australians is to be fine team players. Driven by press and Nobel prizes, we tend to overestimate the individual scientist. Good science thrives on good team work, such as we have come to expect at Curtin, where in our field stands John de Laeter, the head of a productive group. In the happy memories of those who served the International Commission for Atomic Weights and Isotopic Abundances remain the years of de Laeter's innovative and effective leadership towards quantified reliability of data (Peiser *et al.* 1984, 1996). We know he has exerted similar influences in Australia. Generally speaking, we all wish for a great future for science in Australia supported by its universities. Just as the ancient pyramids in Egypt, the temples of Greece and Rome, and the medieval cathedrals of Europe, so the technical universities today give evidence to posterity of the cultural pinnacles exalting their respective periods of history.

Foundations for Today's Achievements in Science were Laid in the Past

I am neither historian nor philosopher and realize that, even for experts, there exist undecipherable complexities in every past epoch. Nevertheless, I dare to focus

on a few developments in history that happen to have struck my attention (Tanton 1958).

We all know of the wealth of ideas that were developed in classical Greek and Roman times. By comparison, the Western European Middle Ages are faulted. Yet, in Bartholomew's 13th century *De Proprietatibus Rerum* we are given a catalogue of observations pertaining to "heaven and earth, beasts, birds, stones, metals, and other substances". The forward momentum in arts and sciences during the renaissance period was initially due to the rediscovery of Greek ideas. The playful Muses are superlative models for originators in the arts and sciences. These ideas themselves, however, were based on sparse observation of nature. By detailed observations begun during the 'dark ages', some of Aristotle's and other Greek postulates were successfully challenged.

Allow me here to anticipate three of my impressions:

- Progress in science is made in very small steps. As Sir Lawrence Bragg used to tell us; "scientists ask only simple questions". Answers, if any, can only come in tiny steps (Thomas & Phillips 1960).

- My second theme is this: knowledge coupled with intuition leads to descriptions of nature. Careful measurement, however, often fails to fit exactly with that description. A forced small modification of our understanding then brings a slightly better description of nature. It is surprising that these modifications are often anticipated by eccentric scholars (De Laeter *et al.* 1992). No better example is that of Democritus' atomic theory; its reality remained an unsubstantiated speculation for many centuries.

- My third concern is that religion and science have great difficulty in engaging in a constructive dialogue aiming at mutual understanding. Religions ask complicated general questions, often answered by trusted divine revelation and accepted, though not without difficulty, by a believing public (Luyckx 1991). Let us recognize that highest achievements of mankind in the fine arts, literature, music, education, philosophies, psychology,

as well as in architecture have come in association with religion.

In the historic past, deeply religious people have also been the principal contributors to science. The well known controversy between the geocentric versus heliocentric doctrines was carried on both sides by Christian leaders. In the 15th century Nicholas of Cusa, a bishop, was by time and concept well in advance of Copernicus in proclaiming "the earth is a sphere, like many celestial bodies, in a cosmos of which the center is everywhere and the circumference nowhere." Established religion did not oppose him, at least not for that speculative philosophy. The first serious conflict with science came when Copernicus showed with inescapable logic that a heliocentric universe must have a radius much larger than demanded by Aristotle's model. Was there fear that a large universe devalued the importance of the human race?

De Laeter's group and other astronomers have in recent years enormously further enlarged the universe that fits very detailed evidence and ties astronomy closely into terrestrial chemistry (De Laeter 1990). Other scientists in this century elucidated the wonderful atomic-scale structures a million times smaller than is open to the unaided human eye or imagination. The earliest experimental investigation into the relationship between the atomic and macroscopic scales was by Johannes Kepler in the 17th century book on snowflakes with the title *De Nive Sexangula* (Senechal 1990).

De Laeter's group, again, and other geologists have given overwhelming evidence by experimentation with radioisotopes that the earth's creation exceeds by a large factor any time span one can piece together from the Bible's pages (Faure 1977). It would be heresy - as Albert Einstein implied - to suggest that our Creator might have planted evidence to deceive us into deducing an erroneous age of our world!

Biology, since the middle ages, has been a beautiful descriptive science. In that mode, especially with the aid of microscopes, it continues to thrill us and bonds our wonderment of nature to that of our children. Biology added new vistas by the genius of Pasteur whose 100th anniversary we observe right now. He showed the idea of spontaneous creation to be false and physiological processes to be chemical reactions. In a recent speech, Arthur Kornberg told how biologists then became microbe hunters (Kornberg 1995), later virus hunters, recently enzyme hunters and now gene hunters. All objects of these hunts aim at chemical entities. Let us thus declare biology now open to de Laeter's experimentation with isotopes.

Allow me just to enumerate some dazzling new scientific insights gained in this century. A million times shorter intervals than we can intuitively grasp are shown to dominate the changes within our cells. We see beauty principally in patterns of audible sounds and visible light. Intuition or divine revelation might lead us to their appreciation, but hardly to patterns of other radiations with far smaller and far larger energy quanta than those of light. Scientists have shown that the earth's biosphere is narrowly limited also in temperature and pressure compared with the enormous ranges of those quantities experienced in our universe. All physical entities are

found to be 'grainy' by nature. Even more bizarre to intuition appear some descriptions of subatomic- and galactic-scale phenomena that nevertheless ring true by their precise fit with observations and the power of successful predictions.

All that leaves individual humans within the real wonders and opportunities of creation with a place that is exceedingly modest, probably not even unique. Religions the while hold on to an instinctively attractive view of preeminence in creation with rewards of Heaven and threat of Hell to assure moral behavior of mankind. From earliest times, the defense of traditional religious views turned beautiful legends and practical rules into dogmas, litmus tests for the faithful.

In a world governed by uncertainty, is the long-term survival of features of our DNA inscribed inheritance not miraculous and adequate comfort to our souls? Do we not see in the trillions of individually living, predominantly cooperating cells in our bodies, a clue that association of human populations could lead to a higher being more worthy of the spirit creation? Are we not ready to concede of the possibility that the evolution of galaxies, isotopes, and all objects in-between are perhaps step by tiny step in principle explainable by the laws of physics and chemistry? We expect to fail in explaining the infinite detail.

Let me take one more look back into the 18th century, when Joseph Priestley is remembered for discovering oxygen. For many historians he was even the founder of modern chemistry. Perhaps he would have described himself primarily as a philosopher, who in Fruchtmann's words (Gibbs 1965) "believed [science] was a vehicle, a conduit, by which human beings may best understand the universe as God had originally intended and created it. The more people learned of the fundamental nature of matter, the better informed they would be about the direction of human life."

Priestley did not live to hear of the discovery of the full elemental set of 90 building stones of matter. To following generations each chemical element had just one kind of atom. As de Laeter has pointed out, it was lucky indeed that this simplification was approximately true. Had it not been so, the development of chemistry would have been delayed until the discovery and separation of isotopes. I believe this because, even after Theodore Richards convincingly proved that there are different leads, the majority of chemists into the latter half of this century regarded atomic weights as constants of nature. De Laeter not only corrected that fallacy, but also propounded the idea that time has now come to turn the problems of isotopes into great opportunities (De Bièvre *et al.* 1993). One of these is to make all chemical analyses much more accurate through isotope-dilution mass spectrometry. So, with others, de Laeter leads science, technology, and commerce to more comparable chemical measurements, firmly bonded to the international system of units.

Further simplification of our understanding of nature showed the elements, the 90 'building stones' of all matter, all to have just three constituents. This simplifying step brought to light more beauties of nature as well as a multitude of deeper questions. Another example of a 'simplification' of our view of nature resides in our own

complex inheritance. It is spelt in an atomic-scale code composed of just four molecular 'letters', and the vast multitude of enzymes are built from just twenty types of amino acids specified by sequences of these four 'letters'.

What now comes later?

At the start of this paper, I correctly described myself as neither historian nor philosopher; for the last portion, with even more justification, I disclaim prophetic talent. However, I take heart from the fact that science has always failed to predict its important consequences. Administrators and politicians, nevertheless, keep trying to predict. They are encouraged, though perhaps misled, by the fact that from scientific progress often emerge some 'certainties', especially for successful applications to industry. De Laeter's isotope work is rich in such potential benefits. Progress, however, remains delayed by expense of instruments and failure of industrial entrepreneurs to grasp the full potential for profitable production of a great variety of materials enriched in and preferably certified for specific isotopes. Eventually this work will surely lead to much more reliable chemical measurements of all kinds, more varied medical test programs and cures. Many of these developments come much more slowly than can reasonably be anticipated. Thirty years ago I would have derided a suggestion that in 1995 physicists would still have to persuade the US Congress that fusion research is a bargain, although it does not yet contribute to the availability of isotopes or to the world's vast power needs.

I marvel at the thermodynamic balances between the innumerable compounds, built up mainly from four types of atoms on a carbon skeleton and a water solvent. These compounds execute virtually all processes in living plants and animals without unduly disturbing the temperature and balance of these amazing systems. Might there be temperature ranges in which similar skeletons of, say, nitrogen (with ammonia as solvent), or of boron (perhaps with B_6H_{10} as solvent), or of silicon (with carbon disulfide as solvent) yield compounds of comparable diversity and catalytic activities? Might such systems produce a kind of 'life' found in other worlds? Even further removed from current research goals is a consideration of electron-orbital systems in which energy barriers to chemical reactions are lowered by substitution of extranuclear electrons by mesons. As far as we know, nature does not widely employ such systems. I would not dare to speculate further on applications for Bose-Einstein condensates or quantum teleportation. When the current 'spin crisis' is resolved, the new insight may well have every-day applications?

A wonderful legend, not unlike that of Adam and Eve, tells that despite Prometheus' warning, Epimetheus opened the box of the lovely Pandora (Mercatante 1985). That box contained all that is evil. All that evil escaped. Likewise - despite warnings of the scientific community - the evil of a nuclear bomb, a fallout of science, will surely be let off as a terrorist's weapon within some of

our life times. We have again but hope, as hope alone was left in the box when Pandora herself replaced the lid.

Hope alone is left to us as we grieve over the history of devastating wars and bruising disagreements between theology and science, with the general public intuitively on the side of religions. As the weapons of war have become potentially lethal to entire populations, science has been widely blamed. Science also came to some bitterly contested conclusions that by logical reasoning have become inescapable. Among them is that not every seed designed for life can be given the environment or species-specific nurturing to mature. Mature individuals deserve and need support and comfort in the harsh competitive existence. Communities will thrive only by care for their individuals and their environment. Thus, to secure further evolution rather than disaster for our human destiny, scientists must join with leaders of religion, the guardians of moral codes of thinking men and women, to recognize, believe, seek, and praise nature as revealed by observation. Alas, this very hope, remains a heresy to the majority of fellow men and women. Yet, for a progressive destiny of human life on our earth, such philosophies are needed to connect with the insights of John de Laeter and other contemporary heroes of science.

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High-accuracy mass spectrometry for isotopic abundances

E L Garner

National Institute of Standards and Technology, Gaithersburg, MD 20899 USA

Abstract

A measurement program was initiated at the National Bureau of Standards (USA) in 1957 to determine the isotopic abundance of the actinide elements with high accuracy. By 1960 it was apparent that high-accuracy isotopic abundance measurements could provide valuable support for a determination of the Faraday constant and the proposed unified atomic weight scale. Of particular interest was the long-term need for more accurate measurements to resolve differences between chemical and mass spectrometric atomic weight determinations as well as significant differences reported for mass spectrometric measurements on the same element. The methodology developed was based upon the integration of analytical chemistry and mass spectrometry into a single measurement process. Analytical chemistry was utilized to mix accurately known quantities of chemically and isotopically pure separated isotopes to produce standards of known isotopic abundance which were used to calibrate the mass spectrometers. Over a period of more than twenty years high accuracy measurements were made to certify the isotopic abundance of uranium and plutonium and to determine the atomic weight of 14 different elements. The uncertainties of these measurements were reported as overall limits of error at the 95% confidence level and represented the sum of uncertainty components for the ratio determination and the components covering effects of known sources of possible systematic error.

Introduction

From the infancy of mass spectrometry, as benchmarked by "positive ray analysis," instruments have been available to make the three types of measurements which are typically made on a modern mass spectrometer. These measurements may be generally classified as the determination of the relative masses of ions, the determination of relative isotopic abundances, and the study of ionization processes and basic phenomena. Highly accurate mass measurements were made early in the history of mass spectrometry by using either the elements, hydrocarbons, oxides or hydrides of the elements, or combinations of the above, to establish a mass scale. The accuracy of this type of measurement was validated long ago, and is widely accepted and recognized.

With respect to isotopic abundance measurements, the realization of high accuracy was a much slower, and perhaps even more tortuous process. Some of the lack of progress can be attributed to a long-standing perception that highly reproducible relative isotopic abundances were adequate, since there was only limited need for accuracies approaching 1 in 10^4 . Another barrier to progress was the limited sensitivity of photographic plates and the early generation of electrical detection systems in characterizing and identifying effects which could bias isotopic abundance measurements by as much as several percent. Many of the measurements made between 1930 and 1960 for specific elements were perceived as self-consistent, although the overall or expanded uncertainties of the measurements were large (several percent) and did not overlap. The practice of reporting only an estimate of the random component of

the uncertainty, rather than completely characterizing all known sources of uncertainty and relevant influence factors contributed to the perception that certain types of mass spectrometers were absolute measuring devices. In particular, surface and thermal ionization mass spectrometers were perceived as absolute measuring devices until a series of measurements at the US National Bureau of Standards (NBS; National Institute of Standards and Technology (NIST) since 1988) in the early sixties provided reasonable and credible scientific evidence that isotopic fractionation in the ion source was an effect which had to be evaluated for each element and set of measurement conditions. As the general knowledge of analytical mass spectrometry improved, it was indeed clear that calibration was necessary and essential, if overall or expanded uncertainties approaching 1 in 10^4 were to be realized.

The need for high accuracy

With the advent of the "atomic/nuclear age," there was an immediate and undeniable driving force to realize high accuracy isotopic abundance measurements. It was well recognized that the numerous working standards and reference samples required for the development and application of nuclear energy would have to be underpinned by a smaller number of well characterized Certified Reference Materials (CRMs) and Reference Materials (RMs). From an economic and security point of view, the need for measurement standards was crystal clear in the accounting, control, lease, sale and use of both unprocessed nuclear materials and processed special nuclear materials for defense and non-defense applications. Because of the national and international use of nuclear technologies, a comprehensive system of CRMs and RMs was proposed to link the variety of mass spectrometers and other instruments characterizing the materials

produced by either production or experimental processes to common reference points. In recognition of the needs of the nuclear industry, and at the request of the US Atomic Energy Commission, the NBS established a uranium isotopic standards program in 1957. Although the principal focus of the program was uranium, plutonium, and other actinides, the knowledge gained and the lessons learned would impact an NBS atomic weight program which emerged just a few years later, and thrived for more than two decades.

Another driving force creating a favorable climate and giving impetus to advances in isotopic abundance measurements was the development and adoption of a unified atomic weight scale. Prior to 1961, two scales were in common use for the reporting of atomic weights. These were designated as the chemical scale, where the natural mixture of oxygen was taken as equal to 16 and the physical scale, where ^{16}O was equal to 16. Effective as of 1961, a new unified atomic weight scale based upon 12 as the assigned atomic mass of ^{12}C was adopted. Values on the chemical scale and the physical scale were systematically reduced by 43 parts per million and 318 parts per million, respectively, to correspond to the ^{12}C scale. All of these changes were included in the 1961 International Table of Relative Atomic Weights which was based on a comprehensive and thorough review of experimental data and evidence reported between 1925 and 1961. At the beginning of this period, atomic weights were determined exclusively by chemical methods. However, by 1961 practically all new values were determined by mass spectrometry. The mass spectrometric values were, with but few exceptions, based on relative isotopic abundances rather than mea-

surements calibrated for the effects of bias in the mass spectrometry. Consequently, there was a critical need for new data and, if at all possible, calibrated or "absolute" measurements to resolve the differences in mass spectrometric data reported for the same element, as well as discrepancies between chemical and mass spectrometric determinations of atomic weights.

Transition to atomic weights determined by mass spectrometry

Having played a significant role in the adoption of the unified atomic weight scale, and having exercised a similar role in the review process leading to the 1961 International Table of Relative Atomic Weights, NBS had great interest in redetermining the atomic weights of key elements. In particular, the focus was on those elements which could be used to assess the accuracy of many of the chemically determined atomic weights. In fact, NBS had a long and distinguished history of research on the atomic weights of the elements. Noyes (1907) reported the first of these measurements, a value of 1.00783 for the atomic weight of hydrogen based on the classical method of the electrolysis of water. Very shortly thereafter, Noyes & Weber (1907) reported the atomic weight of chlorine. This was of particular importance since contemporary work at Harvard on the ratio of silver to chlorine had led to the determination of the atomic weights of a number of elements based on the atomic weight of chlorine. The work on chlorine was followed a few years later by Weber's (1913) publication reporting the atomic weight of bromine. Between 1913 and 1959, work on the atomic weight of a variety of elements was conducted using classical chemical methods. In 1959, NBS was on the verge of starting a program which would within 5 years result in the atomic weights of silver (Shields *et al.* 1960), chlorine (Shields *et al.* 1962), and bromine (Catanzaro *et al.* 1964). The analytical methodology was based upon the use of isotopic standards of known composition which were prepared by gravimetrically blending chemically pure and very nearly isotopically pure separated isotopes of the elements.

The significant event that moved NBS away from a narrow focus on the isotopic abundances of uranium and plutonium to other elements of the periodic table was a broad based program in science to improve our knowledge of the fundamental constants. High accuracy determinations of the Faraday constant were of particular interest because of its relationship to Avogadro's constant. Historically, the Faraday was determined by reacting a pure substance electrolytically with an assumed efficiency of 100%. While the electrochemical data of the time were evaluated as self-consistent, they did not agree as well as needed with the Faraday calculated by combining other fundamental constants. In an effort to bring some clarity to this situation, Craig *et al.* (1960) conducted experiments leading to a determination of the electro-chemical equivalent of high purity silver and a value for the Faraday using a silver perchloric acid coulometer. The work of Craig and his coworkers had critical implications for Avogadro's constant, the Faraday constant and the atomic weights of a number of elements as determined chemically by their combining

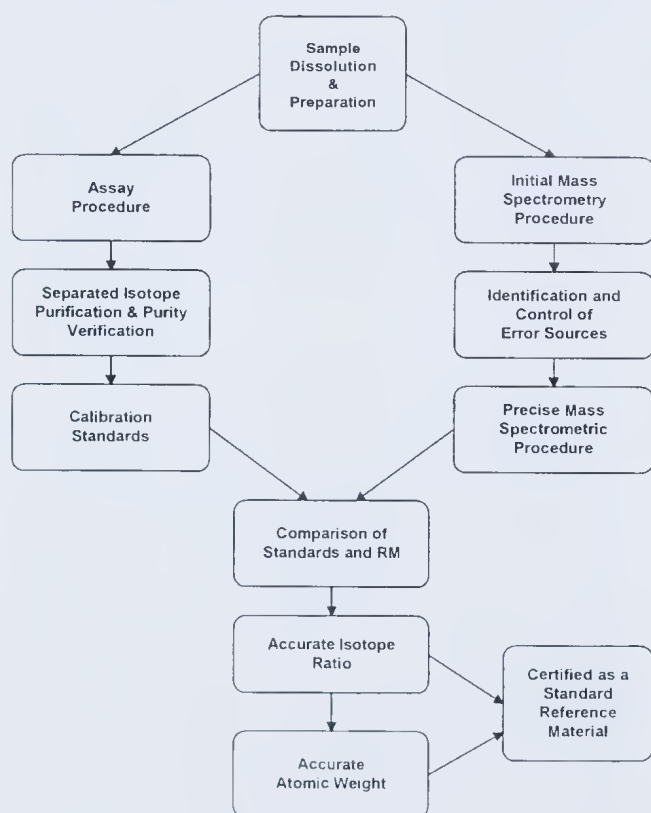


Figure 1. Analytical methodology for high accuracy isotopic abundance.

weight ratios. The initial task for mass spectrometry at NBS was to give assurance that the process used to purify the silver for Craig's measurements had not produced either an isotopically enriched or depleted high-purity silver sample. Because mass spectrometry gave credible evidence that some enrichment of the light isotope did occur, it was deemed necessary to do the following;

- (1) establish the absolute isotopic abundance of silver used in the electrochemical determination of the Faraday;
- (2) establish limits for natural isotopic variations of silver; and
- (3) shed some light on the nearly 8% range in mass spectrometric data reported between 1948 and 1959. At the conclusion of these measurements, the extension of the program to the atomic weights of chlorine, bromine and other elements was an obvious outcome.

The methodology for high accuracy

By 1960, all of the essential and critical technologies for high accuracy were in place and tested. The nuclear community had served as a great incubator for analytical chemistry, mass spectrometry and instrumentation advances. The proof of principle in blending highly enriched separated isotopes to produce standards of known isotopic abundance had been conclusively and routinely demonstrated at uranium diffusion plants where mass spectrometers equipped with electron impact ion sources had made measurements with expanded uncertainties between $5 \text{ in } 10^4$ and $2 \text{ in } 10^4$. The most critical technology for the development of high accuracy uranium isotopic abundance measurements was the availability of relatively large amounts (kilograms) of highly enriched separated isotopes of uranium. The electromagnetic separation technology which produced these nuclear materials also resulted in the availability of economically affordable, but in some cases still very expensive, highly enriched and chemically pure separated isotopes of many other elements. These separated isotopes were the key ingredient for preparing standards of known isotopic abundance to calibrate mass spectrometers for the effect of bias for a wide range of elements other than those of critical and immediate importance to the nuclear industry.

The methodology to determine the isotopic abundance of an element with high accuracy (Fig 1) is in fact a combination of analytical chemistry and mass spectrometry. The least recognized, and perhaps least appreciated component, is the analytical chemistry. The ultimate products from the analytical chemistry are;

- (1) a high purity Reference Material to be calibrated, and
- (2) a series of "calibration standards" with known isotopic ratios covering the range of isotopic ratios of the Reference Material to be characterized.

The critical components and potential sources of uncertainty in the analytical chemistry are sample dissolution, stoichiometry, chemical purification, interfering ions, gravimetry and high precision assay of the separated

isotope solutions for the analyte element. Using gravimetric procedures, weighed aliquots of the separated isotope solutions are blended to produce the calibration standards. Knowing the assay or concentration of the analyte element in the separated isotope solutions, the weight of aliquots blended to produce the standards, and the composition of the separated isotopes from mass spectrometric analysis, the isotopic abundance of the calibration standards can be calculated. Ideally, it is desirable to know the calibration standards with an expanded uncertainty of $1 \text{ in } 10^5$. More realistically, the uncertainty contribution from the calibration standards was $1 \text{ to } 2 \text{ in } 10^4$.

Mass spectrometry instrumentation and procedures

For most of the high-accuracy work at NBS, solid sample, thermal or surface ionization mass spectrometers were used. A notable exception was by Barnes *et al.* (1975) for the isotopic abundance of a reference sample of high purity silicon by electron impact ionization of a gaseous sample. The other notable exception was the use by Gramlich *et al.* (1973) of a double magnetic stage instrument arranged in an "S" configuration and equipped for pulse counting detection. For the atomic weight determination of nickel by Gramlich *et al.* (1989), a commercially designed multicollector instrument was used. Otherwise, all mass spectrometers were single focussing, magnetic sector instruments, either 15 cm or 30 cm radius of curvature, and/or 60° , 68° , or 90° sectors. These instruments (Shields *et al.* 1967) were equipped with interchangeable and nearly identical electronic components, the same basic design of a multi-element, deep-bucket Faraday cup collector, and either a standard Nier type ion source (prior to 1964) or a thin lens "z" focussing ion source (after 1964).

Mass spectrometric procedures for all elements were based upon:

- (1) a knowledge of the sources of uncertainty in the measurement process;
- (2) control of the parameters and influence factors which could contribute to the uncertainty or bias the measurement;
- (3) identifying and selecting the critical analytical parameters; and
- (4) establishing an acceptable tolerance specification for each parameter which would be the same for all analyses.

Because of isotopic fractionation effects in the ion source of a thermal ionization mass spectrometer, it was critical to develop a methodology which yielded precisely the same isotopic fractionation pattern for each analysis. The goal was to quantify the correction for this effect as an experimentally determined constant which was unique for the analytical conditions of the measurement. In general, three types of isotopic fractionation trends or patterns were observed for the ratio of the lighter to heavier isotope of an element:

- (1) constant and non-changing with time;
- (2) decreasing with time; and
- (3) increasing with time.

For some elements and matrices, all three patterns could be observed in the same analysis. By controlling the time base for each analysis and the other critical parameters of the measurement process, it could be demonstrated that the same correction for isotopic fractionation could be applied to each analysis. In addition to isotopic fractionation, it was necessary and essential to characterize the effect of secondary electrons in the collector as well as non-linear effects in the entire measuring system. Complete characterization of the measurement uncertainty from the mass spectrometry included an evaluation of possible sources of uncertainty, influence factors and suspected influence factors in the sample handling system, the ion source, analyzer, ion detector, and the data handling system. A graphic representation of the general scheme used to completely characterize the uncertainty is shown in (Fig 2), including an allowance for the use of judgment-based limits. Knowledge of influence factors and suspected influence factors was integrated into the measurement process as a modification or refinement of control procedures or specifications for control of a parameter.

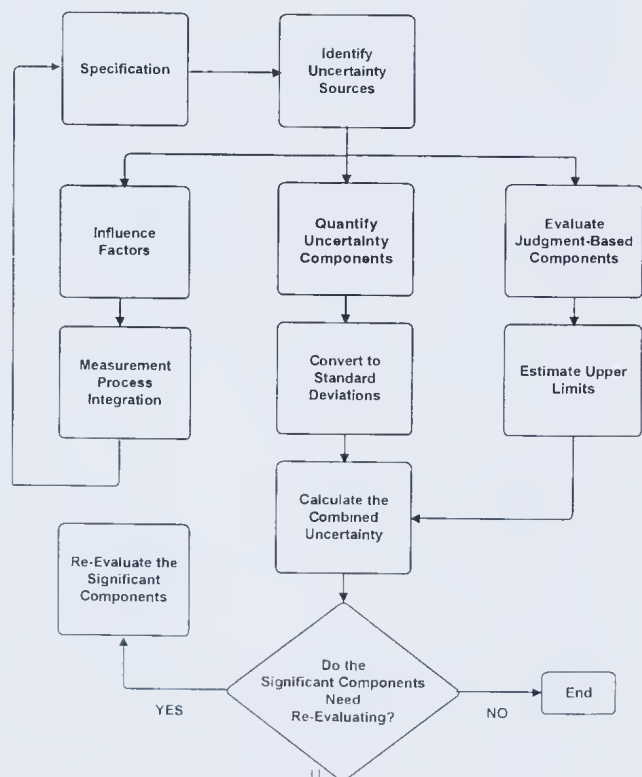


Figure 2. Characterization of measurement uncertainty.

Results

Atomic weight determinations, certification of the isotopic abundances of uranium and plutonium, and trace element analysis by isotope dilution mass spectrometry were the broad areas where high accuracy isotopic abundance measurements were made at NBS from 1960 to 1985. The scope of this paper does not permit full attention to either of these areas, so atomic weights will be used as the prime example. During the period in question, the atomic weights of 14 different elements were determined.

These measurements included; silver (Shields *et al.* 1960); chlorine (Shields *et al.* 1962); copper (Shields *et al.* 1964); bromine (Catanzaro *et al.* 1964); chromium (Shields *et al.* 1966); magnesium (Catanzaro *et al.* 1966); lead (Catanzaro *et al.* 1968); rubidium (Catanzaro *et al.* 1969); boron (Catanzaro *et al.* 1970); rhenium (Gramlich *et al.* 1973); silicon (Barnes *et al.* 1975); potassium (Garner *et al.* 1975); Thallium (Dunstan *et al.* 1980); silver (Powell *et al.* 1981) and strontium (Moore *et al.* 1982). After the period in question, the absolute isotopic abundance ratios and the atomic weight of gallium (Machlan *et al.* 1986) and nickel (Gramlich *et al.* 1989) were reported. The absolute isotopic abundance ratios for a representative number of these elements are shown in Table 1.

Table 1.

Absolute isotopic abundance ratios by thermal ionization mass spectrometry.

Element	Year	Ratio	Value
Ag	1960	107Ag/109Ag	1.0755 ± 0.0013
Ag	1961	107Ag/109Ag	1.07597 ± 0.00135
Br	1964	79Br/81Br	1.02784 ± 0.00190
Cu	1964	63Cu/65Cu	2.2440 ± 0.0021
Rb	1969	85Rb/87Rb	2.59265 ± 0.00170
Re	1973	185Re/187Re	0.59738 ± 0.00039
Tl	1979	205Tl/203Tl	2.38714 ± 0.00101
Ag	1981	107Ag/109Ag	1.07638 ± 0.00022

The uncertainty of an isotopic ratio was reported as an overall limit of error and was determined by summing the 95% confidence limits of the uncertainty components. The overall or expanded uncertainty of the measurement included terms to cover random effects as well as possible systematic error. Each overall or expanded uncertainty included a random component for the "mass spectrometric analytical error," a component for "possible systematic error in composition of separated isotopes," and a component for "possible systematic error in chemical analysis." The only notable exception was the atomic weight of silver by Shields *et al.* (1960) which included a component for nuclidic masses, since at that time it was not clear as to whether the unified atomic weight scale would be adopted. Because rounding-off could have impact on the atomic weight calculation, most ratios were reported to one figure beyond significance.

While there is some uniqueness about each of the measurements in the atomic weight series, silver is considered in a separate niche because;

- (1) it had the distinction of being the "pathfinder element" (Shields *et al.* 1960) of the series;
- (2) the only element for which additional measurements were made and data published beyond the original measurements (Shields *et al.* 1961); and
- (3) the only element for which a completely independent redetermination was made by a different team of scientists (Powell *et al.* 1981).

In addition, silver was the only element for which the expanded uncertainty was perceived to be very near the limits achievable with the instrumentation, analytical chemistry and measurement process then developed.

Discussion

The single unifying concept which brought together the critical elements of analytical chemistry and mass spectrometry to yield high accuracy isotopic abundance measurements was the concept of measurements as a process. Pontius & Cameron (1967) first documented this concept in describing mass measurements as a production process. A fundamental assumption of this concept is that measurement is analogous to a production or manufacturing process. When a production process is in a state of control, the product is uniform and reproducible, reflecting the degree of control of the process. Analogous to the industrial production process, the product of an isotopic abundance measurement process is an isotopic ratio. When the entire process is in a state of statistical control, the associated uncertainty of the process is valid and predictable. When the measurement process is out of statistical control, predictability is lost and the uncertainty of the measurement under control conditions is not applicable to the out-of-control condition.

In conjunction with measurement as a process, the concept of measurement assurance was the other general principle which underpinned the pathway to high accuracy isotopic abundance measurements. This process was perceived and implemented as a continuous improvement process. The technique for mass spectrometry included but was not limited to;

- (1) the use of sound experimental design principles so that the entire measurement process, its components and relevant influencing factors could be well characterized, monitored and controlled;
- (2) complete experimental characterization of the uncertainty for the measurement process to include statistical variations, contributions from all known or suspected influence factors, imported uncertainties, judgment based components, and the propagation of uncertainties throughout the measurement process; and
- (3) continuously monitoring the performance and state of control of the complete measurement process, both analytical chemistry and mass spectrometry, with locally tested and proven quality control or process control techniques to include the measurement of stable isotopic abundance check standards along with the normal workload.

The state of statistical control observed for an element did not preclude the measurement assurance requirement to continuously monitor, control, and evaluate the process. After completion of a unique or distinct set of measurements such as an atomic weight determination, then it was appropriate to study, evaluate, test and experiment with the measurement process. The results and findings would then become the basis for changing, improving, redesigning or even developing a substantially different process. After the next set of unique or distinct measurements the cycle was repeated. Where applicable, knowledge gained about one element was utilized in developing and evaluating the measurement process for other elements.

Perhaps the best illustration of the value of a sound measurement assurance program was the first attempt

to determine the atomic weight of bromine in 1962. An independent, third-party statistical analysis of the data, a practice which was followed in all of the high accuracy isotopic measurements, revealed an out-of-control statistical condition during the preparation of the calibration mixes. Re-evaluation of the analytical chemistry revealed that the separated isotopes were not blended over a short time span of hours but a period of several days. As a result the isotopic abundances of the calibration standards were dependent on the time of mixing and it was necessary to void the entire set of isotope ratio measurements. This hard-earned lesson became a cornerstone of the methodology for all future measurements in which solutions were blended to prepare calibration mixes or to perform isotope dilution.

Summary

The products of isotopic abundance mass spectrometry are the value for the abundance ratio(s) and the uncertainty associated with the ratio. Initial isotopic ratio measurements by thermal ionization mass spectrometry at NBS between 1958 and 1960 were made with an expanded uncertainty of 2% over the ratio range 1:20 to 20:1. With major developments and improvements in instrumentation and measurement process, the expanded uncertainty was reduced to 0.5% for the ratio range 1:100 to 100:1. The breakthrough to an expanded uncertainty of 1 or 2 in 10^4 as a realistic limit for high accuracy isotopic abundance measurements by thermal ionization mass spectrometry occurred when it was realized that the best strip chart recorders available were a limiting factor. When performing to manufacturer's specification, strip chart recorders measured a full scale output signal to $\pm 0.5\%$. By modifying the strip chart recorder to operate in an expanded scale measuring mode, the contribution to the uncertainty of the measurement was reduced by a factor of 10. With improvements in the measurement process and the advent of digital measurement systems, the ultimate accuracy for thermal ionization mass spectrometry was realized for the determination of the atomic weight of silver (Powell *et al.* 1981).

In looking at the future from a 1995 perspective, the potential for ultra high accuracy measurements of 1 in 10^5 is still over the horizon. Assuming ideal conditions of equal atom ratio measurements, ultra high enriched separated isotopes of 99.9999%, highly reproducible isotopic fractionation, and ideal ion current intensities, ultra high accuracy is not a practical goal without major breakthroughs or different approaches in the analytical chemistry and mass spectrometry.

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Ultra-high accuracy isotopic measurements: Avogadro's constant is up!

P De Bièvre

Institute for Reference Materials and Measurements, European Commission-JRC, B-2440 GEEL,
and Department of Chemistry, University of Antwerpen, Belgium

Abstract

Ultra-high accuracy isotopic measurements have been achieved on abundance ratios of Si isotopes by achieving 10^{-5} reproducibilities on the ratio measurements and calibrating the results by synthetic isotope mixtures prepared to $2 \cdot 10^{-5}$ combined relative uncertainty. This enabled us to attain a relative combined uncertainty of $3 \cdot 10^{-5}$ on the abundance ratios in natural Si samples and, consequently, 10^{-7} on the Si molar mass. The route to these results is described, followed by a description of the improvement of our knowledge of the Avogadro Constant N_A through these measurements.

Combined with measurements of the lattice constant and density in a near-perfect Si single crystal, Si molar mass measurements lead to a totally independent value of N_A . This value is compared to the authoritative CODATA evaluation of the interrelationships of our fundamental constants. After the year 2000 an improved value of N_A will almost certainly play a key role in a redefinition of the kilogram, our primary standard of mass.

The acquired expertise in measurement instrumentation and measurement procedures for measurements of Si isotope amount ratios can now be extended to a more general use in measurements of isotope amount ratios (*i.e.* in other elements). It can also be combined with isotope dilution. I describe how the latter combination may open the possibility of realising direct traceability of an amount-of-substance measurement to the measurement procedure and instrumentation leading to the Avogadro Constant. Perhaps a "traceability to the mole", *i.e.* to SI, is being developed.

Introduction

Some elements have their abundance ratios known to 10^{-3} combined relative uncertainty, some abundance ratios have been measured to 10^{-4} , but only for one element, silicon, have the abundance ratios been measured to a confirmed relative uncertainty in the 10^{-5} range, all uncertainty components included. It required 10^{-5} reproducibility in abundance ratio measurements, calibrated by $2 \cdot 10^{-5}$ accurate synthetic isotope mixtures, to achieve a $3 \cdot 10^{-5}$ combined relative uncertainty. Since it takes an enormous effort to achieve this, the incentive to do it must be important. Indeed it is.

It is the molar mass M (numerically equal to the atomic weight) which constituted for many years the limiting factor in the knowledge of the Avogadro constant N_A (in mol^{-1}) as determined from X-ray density, lattice constant and molar mass measurements on a near-perfect Si single crystal (an "Avogadro crystal") through the relation

$$N_A = \frac{M(\text{Si}) / \rho}{V_a} \quad (\text{eq. 1})$$

in which N_A is calculated as the ratio of molar volume $M(\text{Si}) / \rho$ (in $\text{m}^3 \text{mol}^{-1}$) to atomic volume V_a (in m^3); M

(Si) is the molar mass in kg mol^{-1} and ρ the density in kg m^{-3} .

The value of V_a is determined through an X-ray interferometric measurement of the lattice constant d_{220} . With the lattice parameter $a_0 = d_{220} \sqrt{8}$, the atomic volume $V_a = a_0^3$. Molar masses are derived from isotope abundances f_i ($\sum f_i = 1$) and atomic masses $M(^i\text{Si})$. In fact, abundance ratios R_{ij} are measured relative to the abundance f_i of one isotope j as,

$$\begin{aligned} M(\text{Si}) &= \sum f_i \cdot M(^i\text{Si}) = \frac{\sum f_i M(^i\text{Si})}{\sum f_i} \\ &= \frac{\sum [f_i M(^i\text{Si})] / f_j}{(\sum f_i) / f_j} = \frac{\sum R_{ij} M(^i\text{Si})}{\sum R_{ij}} \end{aligned} \quad (\text{eq. 2})$$

The isotope abundances (Table 1) and resulting molar mass (Table 2) of natural Si are not constant enough in nature to be used in this approach. Individual calibrated measurements of the Si in the "Avogadro crystal" must be carried out. Combined relative uncertainties which have been achieved on M , V_a and ρ by 1994 in the currently running three Avogadro projects in the world, are summarized in Table 3. A combined relative uncertainty of 10^{-7} on $M(\text{Si})$ requires a combined relative uncertainty of $3 \cdot 10^{-5}$ on the abundance ratios of the Si isotopes in a Si single crystal. Before 1990 this uncertainty was simply the largest uncertainty contributor to the uncertainty of N_A (Table 4).

Table 1

International Union of Pure and Applied Chemistry (IUPAC) isotope abundances of Si.

Isotopes	IUPAC representative isotopic composition of terrestrial material	IUPAC selected "Best Measurement"	IUPAC evaluated range of natural occurrences	IRMM 1993 = IUPAC selected "Best Measurement" in 1995
$f(^{28}\text{Si})$	0.9223 1	0.9223104 46	0.9241-0.9214	0.9223104 46
$f(^{29}\text{Si})$	0.0467 1	0.0467536 33	0.0473-0.0457	0.0467536 33
$f(^{30}\text{Si})$	0.0310 1	0.0309360 36	0.0314-0.0301	0.0309360 36

Table 2

International Union of Pure and Applied Chemistry (IUPAC) molar masses of Si.

Molar mass (atomic weight)	$M(\text{Si})/\text{g}\cdot\text{mol}^{-1}$
IUPAC representative atomic weight of terrestrial material	28.0855 3
IRMM 1993	28.0854349 76
IUPAC selected "Best Measurement" up to 1995	28.0855 2
after 1995	28.0854349 76

Table 3

Achieved combined relative uncertainties on measurements of lattice parameter a_0 , density ρ and molar mass M , as measured on near-perfect Si single crystals. IRMM = Institute for Reference Materials and Measurements, Geel; PTB = Physikalisch Technische Bundesanstalt, Braunschweig; NRLM = National Research Laboratory for Metrology, Tsukuba; IMGC = Istituto di Metrologia Gustavo Colonnetti, Torino.

N_A Project	1	2	3
a_0	PTB ¹ 6 10 ⁻⁸	IMGC ² 3 10 ⁻⁸	
V_a	1.8 10 ⁻⁷	9 10 ⁻⁸	
ρ	PTB ¹ 7.7 10 ⁻⁷	IMGC ³ 1.5 10 ⁻⁷	NRLM ⁴ 1.1 10 ⁻⁷
$M(\text{Si})$	IRMM ¹ 3.2 10 ⁻⁷	IRMM ¹ 3.2 10 ⁻⁷	IRMM ¹ 3.2 10 ⁻⁷

¹De Bièvre *et al.* (1995); ²Basile *et al.* (1995); ³Saccomi *et al.* (1995); ⁴Fujii *et al.* (1995)

Table 4

The isotopic composition of natural silicon with combined relative uncertainties compared with uncertainties of measurements at IRMM on "Avogadro Si crystal" samples.

IUPAC values for natural abundances			IRMM 1989/90	IRMM 1992 ^a	IRMM 1995 ^b
$f(^{28}\text{Si})$	0.9223 1	$\pm 1 \cdot 10^{-4}$	$\pm 1 \cdot 10^{-5}$	$\pm 1 \cdot 10^{-6}$	$\pm 1 \cdot 10^{-6}$
$f(^{29}\text{Si})$	0.0467 1	$\pm 2 \cdot 10^{-3}$	$\pm 2 \cdot 10^{-4}$	$\pm 2 \cdot 10^{-5}$	$\pm 2 \cdot 10^{-5}$
$f(^{30}\text{Si})$	0.0310 1	$\pm 3 \cdot 10^{-3}$	$\pm 3 \cdot 10^{-4}$	$\pm 3 \cdot 10^{-5}$	$\pm 3 \cdot 10^{-5}$
$M(\text{Si})$	28.0855	$\pm 1 \cdot 10^{-5}$	$\pm 1 \cdot 10^{-6}$	$\pm 1 \cdot 10^{-7}$	$\pm 1 \cdot 10^{-7}$
$n(^{29}\text{Si})/n(^{28}\text{Si})$	0.050 6	$\pm 2 \cdot 10^{-3}$	$\pm 2 \cdot 10^{-4}$	$\pm 2 \cdot 10^{-5}$	$\pm 2 \cdot 10^{-5}$
$n(^{30}\text{Si})/n(^{28}\text{Si})$	0.033 6	$\pm 3 \cdot 10^{-3}$	$\pm 3 \cdot 10^{-4}$	$\pm 3 \cdot 10^{-5}$	$\pm 3 \cdot 10^{-5}$

^aSeyfried *et al.* (1992); ^bDe Bièvre *et al.* (1995)

Measurement of $M(\text{Si})$ and its relative uncertainty

The Si crystal samples were converted to SiF_4 gas as described by De Bièvre *et al.* (1995). The Avogadro I Mass Spectrometer (an IRMM upgraded MAT-CH5) had yielded a $1 \cdot 10^{-6}$ $M(\text{Si})$ uncertainty which had led to $1.1 \cdot 10^{-6}$ relative uncertainty on the 1992 N_A value (Seyfried *et*

al. 1992). Using the acquired experience, an Avogadro II Mass Spectrometer was assembled, essentially based on a standard MAT 271 instrument, into what is now known as the IRMM/MAT 271 Avogadro II mass spectrometer. The development of appropriate measurement procedures in which correction for every single significant error as well as a full orthodox calculation of every

uncertainty contribution was properly incorporated, proved to be of overriding importance. Creating near-to-ideal vacuum conditions, realizing close-to-ideal circumstances for the SiF₄ gas, also proved to be crucial for the ultimate quality of the results and has been described elsewhere (De Bièvre *et al.* 1994). Then, of course, synthetic isotope mixtures had to be made to calibrate the isotopic measurements on the Si of the “Avogadro” crystal. They were made from enriched isotopes (see Table 5) which were incorporated in highly stable, non-hygroscopic, pure Cs₂SiF₆ molecules. This enabled the preparation of isotope mixtures of about “natural” isotopic composition (Fig 1). Typical values of such a mixture with their uncertainties are given in Table 6, which also shows a full analytical uncertainty budget that will ultimately contribute to the uncertainty of the Avogadro constant. The complete correct formula to calculate the value of such a mixture is (De Bièvre *et al.* 1995);

$$\frac{n(^{29}\text{Si})}{n(^{28}\text{Si})} = \frac{\frac{m(^{28}\text{Si}) \cdot f(^{29}\text{Si})}{M(^{28}\text{Si})} + \frac{m(^{29}\text{Si}) \cdot f(^{28}\text{Si})}{M(^{29}\text{Si})} + \frac{m(^{30}\text{Si}) \cdot f(^{28}\text{Si})}{M(^{30}\text{Si})}}{\frac{m(^{28}\text{Si}) \cdot f(^{28}\text{Si})}{M(^{28}\text{Si})} + \frac{m(^{29}\text{Si}) \cdot f(^{28}\text{Si})}{M(^{29}\text{Si})} + \frac{m(^{30}\text{Si}) \cdot f(^{28}\text{Si})}{M(^{30}\text{Si})}}$$

(eq. 3)

Table 5

Isotopic composition of the enriched starting materials “Si” (after chemical purification and assay) as measured on their SiF₃⁺ ions. Combined standard uncertainties (u_c) are given below the digits to which they apply.

	Enriched “ ²⁸ Si”	Enriched “ ²⁹ Si”	Enriched “ ³⁰ Si”
<i>f</i> (²⁸ Si)	0.9953463 10	0.0343310 200	0.0364759 44
<i>f</i> (²⁹ Si)	0.0028138 5	0.9639600 210	0.0028005 43
<i>f</i> (³⁰ Si)	0.0018399 8	0.0018090 11	0.9607236 63

Table 6

Calculated values with combined relative uncertainties for one of the Si synthetic isotope mixtures as propagated from the contributing uncertainty sources. Also listed are the chemical uncertainties for A_r(Si):18.

	abundance (amount of substance fraction) in the synthetic mixture	10 ⁷ combined relative standard uncertainty					
		total	as contributed to the total by the measurements of the:				
			abundances of enriched isotope materials ^a	chemical impurities	stoichiometry	weighings	atomic masses of the isotopes
<i>f</i> (²⁸ Si)	0.9233923 18	18	12	6.5	6.5	8.4	0.2
<i>f</i> (²⁹ Si)	0.0463008 14	14	10	4.6	4.6	6.1	0.14
<i>f</i> (³⁰ Si)	0.0303069 11	11	7.9	3.0	3.0	6.1	0.09
<i>A_r</i> (Si) ^b = 28.0837260 27	1.0000000 1 ^c	25	18	9	9	12	<1

^afrom measurements of the enriched isotopes; ^bthis “sample atomic weight” applies only to this synthetic mixture; ^crounding off uncertainty only.

Table 7

Isotopic composition and silicon atomic weight of the “test material” which is now a certified isotopic reference material (IRMM 018). Combined standard uncertainties (u_c) are given below the digits to which they apply.

Abundance ratio		Abundance (amount of substance fraction)			Atomic weight (relative atomic mass)
<i>n</i> (²⁹ Si)/ <i>n</i> (²⁸ Si)	<i>n</i> (³⁰ Si)/ <i>n</i> (²⁸ Si)	<i>f</i> (²⁸ Si)	<i>f</i> (²⁹ Si)	<i>f</i> (³⁰ Si)	A _r (Si)
0.0508442 24	0.0335851 33	0.9221440 35	0.0468857 21	0.0309703 29	28.085635 6

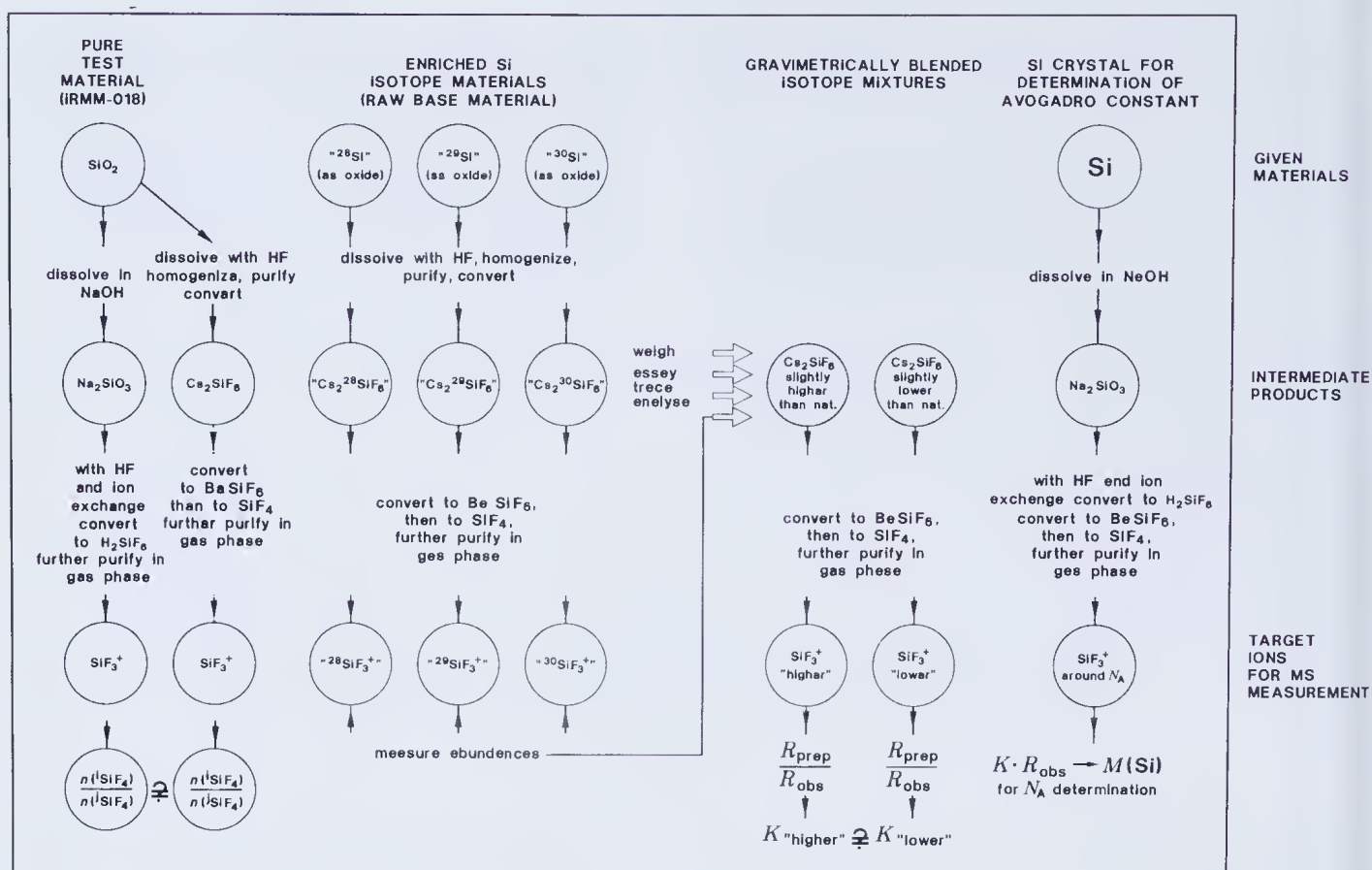


Figure 1. General layout of preparation and measurements of Si isotope mixtures.

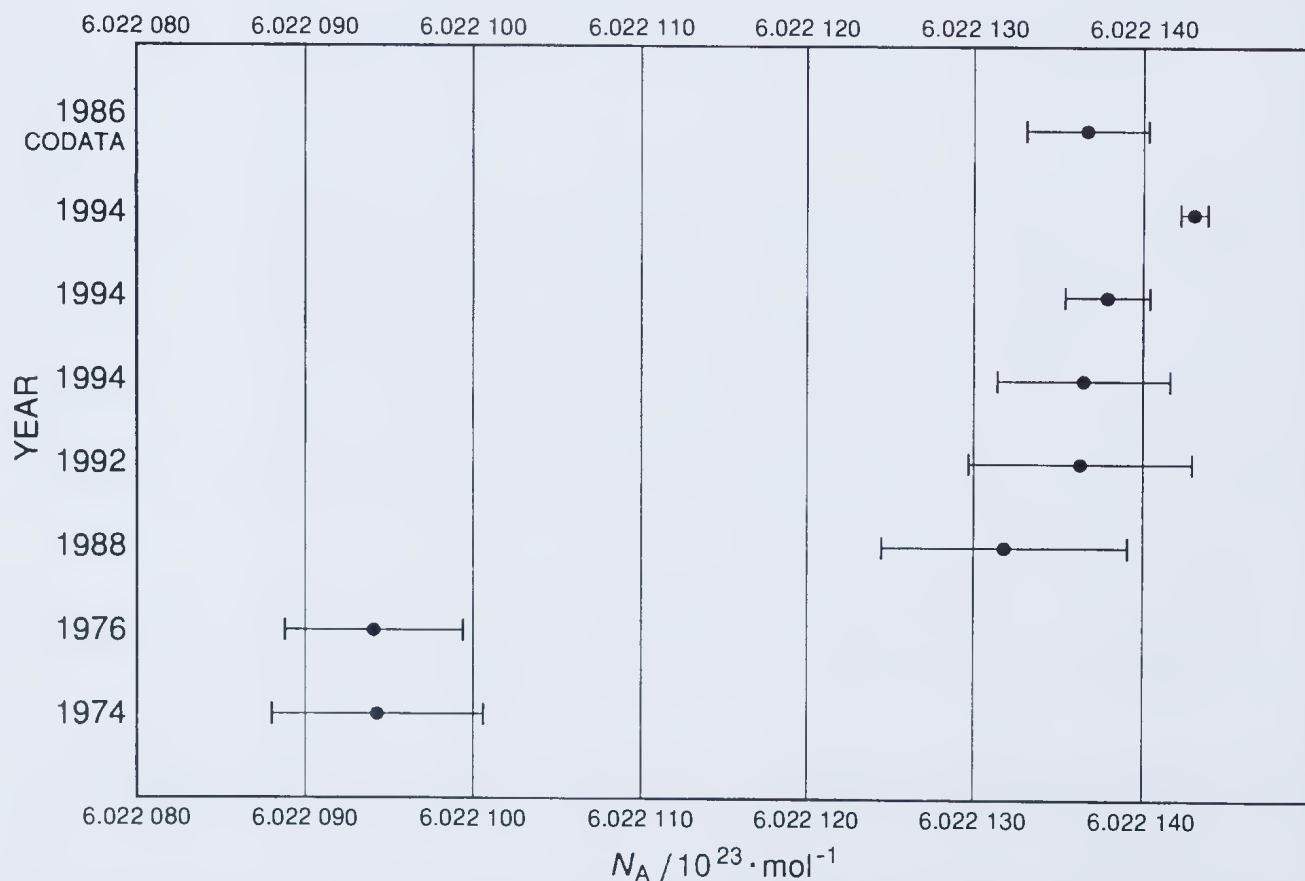


Figure 2. Values and uncertainties (as stated by authors) for N_A in the period 1974-1986. Values are from Deslattes *et al.* (1974, 1976), Cohen & Taylor (1987), Deslattes (1988), Seyfried *et al.* (1992), Basile *et al.* (1995), De Bièvre *et al.* (1995).

where " indicates the isotopically enriched materials, not pure isotopes. In the course of the project, a 10 kg SiO₂ batch was measured and calibrated and made into a certified reference material, IRMM-018 (De Bièvre *et al.* 1994), the values of which are given in Table 7.

What now is Avogadro’s Constant?

The various determinations of N_A over the last 20 years are given in Table 8 and Figure 2. They show the gradual “tuning in” of the value as well as the reduction of the uncertainty. As is apparent from the CODATA evaluation of the interrelationships of the fundamental constants (Cohen & Taylor 1987; Taylor & Cohen 1990), the Avogadro constant obtained through the molar mass/lattice constant/density route is consistent at the $10^{-6} N_A$ level with other fundamental constants such as the Planck constant, the Boltzmann constant, the Universal gas constant *etc.* It is interesting to note (De Bièvre & Peiser 1994) how this uncertainty has been decreasing at a steady rate of a factor of 10 every 15 years since about 1860 (Fig 3).

Table 8

Values of N_A with their combined relative uncertainties as determined in the period 1974-1994, compared to the 1986 CODATA evaluation.

Year	N_A with uncertainty
1974 ^a	$6.0220943 \cdot 10^{23}$ 63
1976 ^b	$6.0220941 \cdot 10^{23}$ 53
1988 ^c	$6.0221318 \cdot 10^{23}$ 73
1992 ^d	$6.0221363 \cdot 10^{23}$ 66
1994 ^e	$6.0221365 \cdot 10^{23}$ 51
1994 ^f	$6.0221379 \cdot 10^{23}$ 25
1994 ^f	$6.0221430 \cdot 10^{23}$ 8
CODATA ^g 1986	$6.0221367 \cdot 10^{23}$ 36

^aDeslattes *et al.* (1974), ^bDeslattes *et al.* (1976), ^cDeslattes (1988),
^dSeyfried *et al.* (1992), ^eDe Bièvre *et al.* (1994), ^fBasile *et al.* (1994),
^gCohen & Taylor (1987).

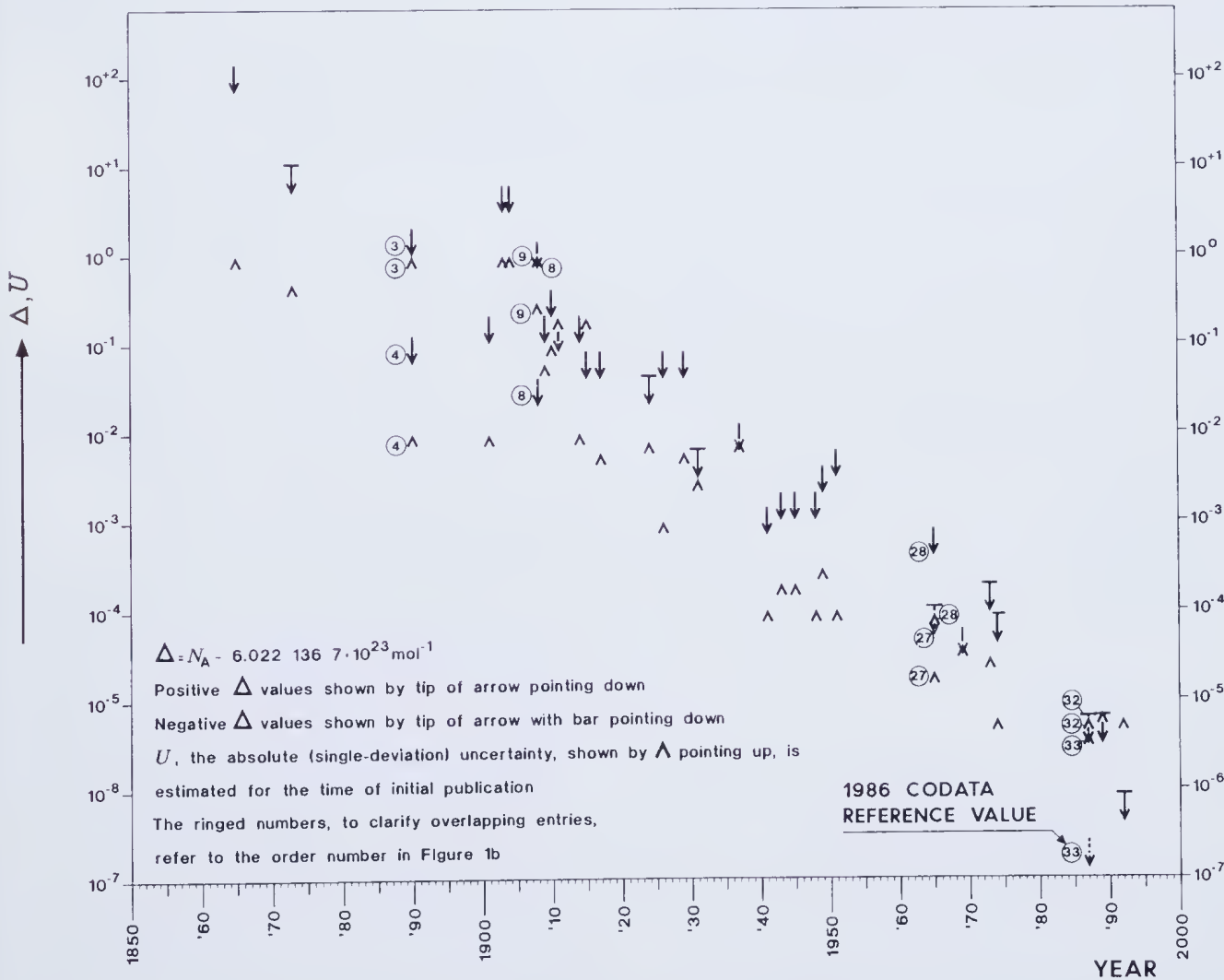


Figure 3. Uncertainties of published values for Avogadro’s constant.

Possible consequences of the achieved uncertainty on N_A

It is now well accepted (Kind & Quinn 1995) that there are variations of the order of 5×10^{-8} kg in the mass of the prototype of the kilogram, our primary standard of mass (see Fig 4). Hence, a new definition of the kilogram is needed. It will probably evolve around “ $1/12$ of the mass of $\{N_A\}$ atoms of ^{12}C ($\times 1000$)”. For a smooth transition of definitions, an uncertainty of at least $5 \times 10^{-8} N_A$ must be attained on N_A . Work is in progress to achieve this.

Inversely, the observation that N_A is consistent with other fundamental constants to better than $10^{-6} N_A$, one could say that the closely-knit network of fundamental constants supports a value of N_A to at least $10^{-6} N_A$ combined relative uncertainty and therefore also supports the claimed combined relative uncertainty of the molar mass, lattice constant and density measurements as a group – not necessarily singly. Hence, this network also supports the measurements of the isotope amount ratios R_i of Si at the 3×10^{-5} R level. Apart from the fact that the molar mass measurements are traceable to prepared isotope amount ratios (synthetic isotope mixtures), the entire measurement procedure to achieve 3×10^{-5} uncertainty on an isotope amount ratio can be said to be, so to say, under the supreme quality control of the Avogadro constant

and its interrelationships with other fundamental constants. There is indeed a strong “quality assurance”; the measurement procedure and instrumentation appear to be monitored by the “network” of inter-related fundamental constants.

Are the measurement methods leading to the Avogadro constant useable for other metrological purposes?

Given the supreme “quality assurance” exerted by the network of fundamental constants on the measurement methods used, the results obtained with these methods are indeed confirmed by this network within the stated uncertainties. Are results of measurements, by these methods, not reliable and credible in other fields of application to within the stated uncertainties? Does the X-ray interferometric method used not yield a result of the same uncertainty in other lattice constant measurements? Are density measurements using the same method on other materials not credible to the stated uncertainty? Are molar mass determinations not reliable to the stated uncertainty when performed on other (ideal) gases? The underlying reasoning for these questions is that measurement methods which are monitored by a quantified connection to the network of interrelated

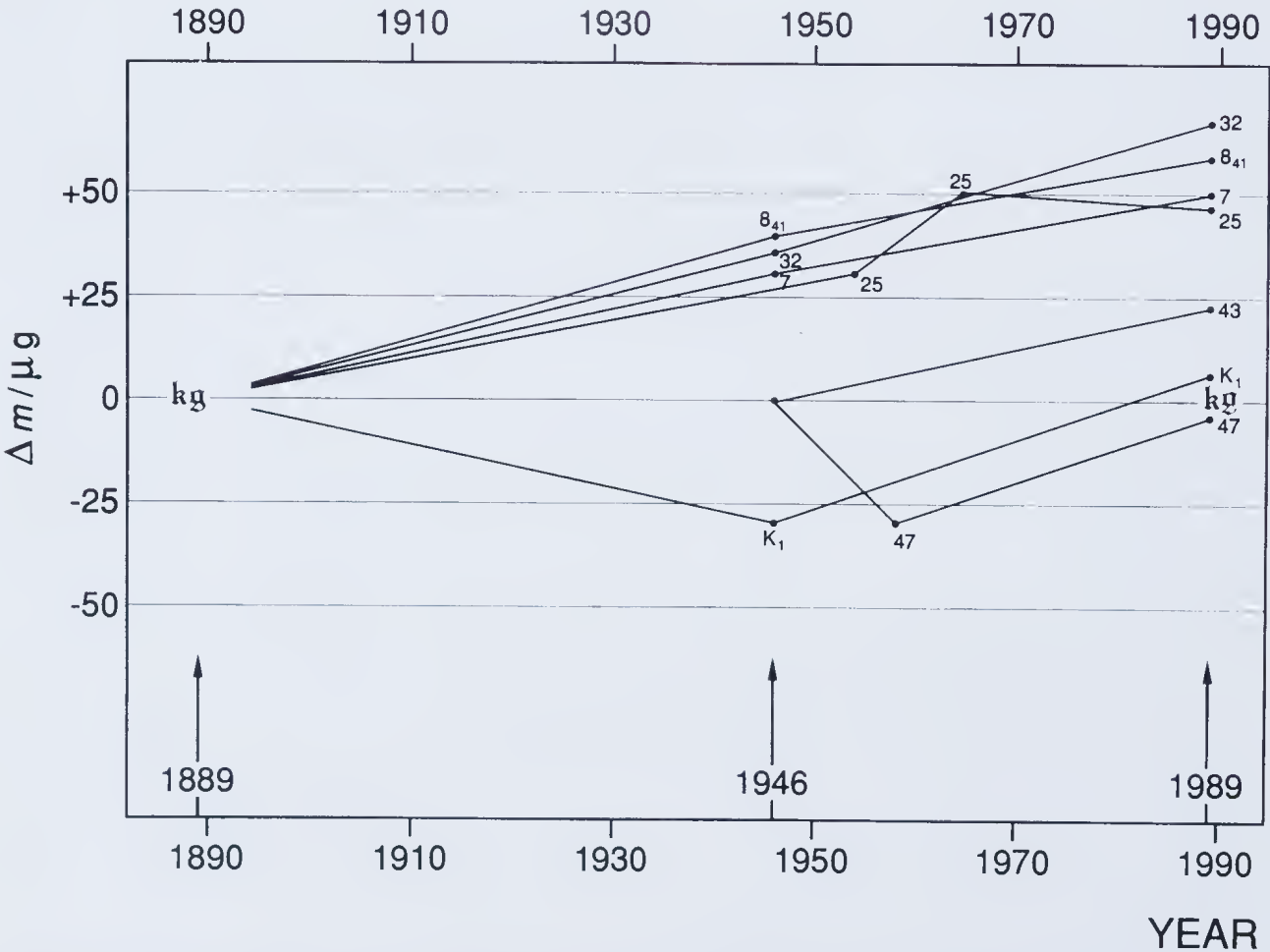


Figure 4. Observed variations in mass of realisations of the kilogram (indicated by their number identification) against the mass of the prototype kg of the kilogram.

fundamental constants are subject to the highest "quality assurance" programme imaginable, one which does not make use of a human convention (written procedure or other) as the ultimate judge but of nature itself by referring to its unalterable fundamental constants.

What is more, all quantities measured in equation 1 are properly traceable to SI units, and, in addition, equation 1 only contains ratios of values expressed in SI units,

$$N_A = \frac{kg \text{ mol}^{-1} / kg \text{ m}^{-3}}{m^3} = \text{mol}^{-1} \quad (\text{eq. 4})$$

This ultimately delivers a number per mole, only based on ratios of values which are expressed in SI units. Isotope mass spectrometrists have always made calibrated measurements of a molar mass (numerically equal to atomic weight or mean relative atomic mass) which were in fact traceable to ratios of amounts of pure isotopes in gravimetric preparations from enriched isotope materials. Through various corrections ε , such as for the lack ε_{is} of 100% isotopic purity of the enriched isotopes, for impurities ε_{imp} and for deviations of stoichiometries ε_{st} of the compounds containing the enriched isotopes, the weight or mass ratio of isotopically enriched materials (E) leading to synthetic isotope mixtures, is converted into an amount ratio of (pure) isotopes;

$$\frac{n(E)}{n(E)} = \frac{m(E)}{m(E)} \cdot \frac{M(E)}{M(E)} \cdot \frac{1-\varepsilon_{is}(E)}{1-\varepsilon_{is}(E)} \cdot \frac{1-\varepsilon_{st}(E)}{1-\varepsilon_{st}(E)} \cdot \frac{1-\varepsilon_{imp}(E)}{1-\varepsilon_{imp}(E)} \quad (\text{eq. 5})$$

Also, this equation only contains ratios (the corresponding uncertainty budget is given in Table 6). The isotope amount ratio then serves to calibrate the measured abundance ratios.

The N_A measurement as a "primary method" for amount ratios

As described above, a completely understood and fully described measurement procedure does result from the isotopic measurements of Si for the determination of N_A . The equations relating "measurement signals" to what is intended to be measured are all in expressed (in ratios of quantities expressed) in SI units and do not contain any empirical term. We think therefore that they qualify as a "primary method of measurement". If so, other amount ratio measurements, using this procedure can also be considered as having been measured by a "primary measurement method" which is subject to the supreme "quality assurance" exerted by the fundamental constants network. Ensuing results thus borrow their credibility and stated uncertainty from that network of fundamental constants.

Consequences for isotope dilution as measurement method

An isotope dilution measurement procedure compares an unknown amount of a representative isotope of an element in a sample X to a known amount ("spike") of a representative but other isotope of the same element in a sample Y (De Bièvre 1990,1993)

through the measurement of an amount ratio R in their isotopic blend B,

$$R_B = \frac{n(E)_X}{n(E)_Y} \quad (\text{eq. 6})$$

All other isotopes in unknown sample and spike are only correction terms to the above equation (De Bièvre 1990,1993). The full general equation is,

$$\frac{n(E)_X}{n(E)_Y} = \frac{R_Y - R_B}{R_B - R_X} \cdot \frac{\sum R_{iX}}{\sum R_{iY}} \quad (\text{eq. 7})$$

The connection of the measurement of a (very) small amount or a (very) small concentration can therefore be visibly and traceably made to a pure substance (the isotopically enriched spike material). This in itself can be expressed in mol kg^{-1} through corrections of mass due to impurities, deviation of 100% isotopic purity, a known (deviation of) stoichiometry and known atomic weights. Alternatively, the spike can be measured by comparing it to a pure substance of natural isotopic composition (reverse isotope dilution). Thus traceability to the value in mol kg^{-1} in a pure substance can be established using a measurement method which in itself is controlled by the Avogadro constant and the network of fundamental constants.

When the kilogram itself has been redefined as the mass of so many atoms as there are contained in 0.012 kg of ^{12}C , exclusive traceability to the mole will have been established since the kg will have disappeared from the traceability chain.

Other evidence for a fundamental role of isotope amount ratio measurements

When measuring the abundance ratios of the Si isotopes on SiF_4 gas, it is obvious that the inlet of the gas into the ion source of the mass spectrometer must be done through pinholes in a (gold) leaf (Fig 5). This process continuously changes the isotopic composition of the gas (actually enriching the sample in the expansion vessel prior to the inlet, in the heavier isotopic molecules). The size of this effect is derived directly from kinetic gas theory; it is the very well known square-root-of-mass-ratio. Performing measurements over many hours, of exponentially changing values of the isotope amount ratio over time or, better, over the continuously measured ion current of one isotope, enables back-extrapolation of the isotope amount ratio to find its value at time zero, the opening of the valve of the sample container. The gas flow rate into the ion source is,

$$-dN_i(t)/dt = \beta \cdot M^{-\Phi} \cdot N_i(t) \quad (\text{eq. 8})$$

where $N_i(t)$ is the number of molecules in the container at $t=0$, and β is a constant for a given effusion barrier. Integrating from t to t_0 yields;

$$N_i(t) = N_i(t_0) \cdot \exp(-\beta \cdot M^{-\Phi} \cdot t) \quad (\text{eq. 9a})$$

and

$$N_j(t) = N_j(t_0) \cdot \exp(-\beta \cdot M^{-\Phi} \cdot t) \quad (\text{eq. 9b})$$

Thus, for isotopic gas molecules, one establishes that,

$$\ln \frac{I_{ij}(t)}{I_{ij}(t_0)} = -\beta \cdot (M^{-\Phi} - M^{-\Phi}) \cdot t \quad (\text{eq. 10})$$

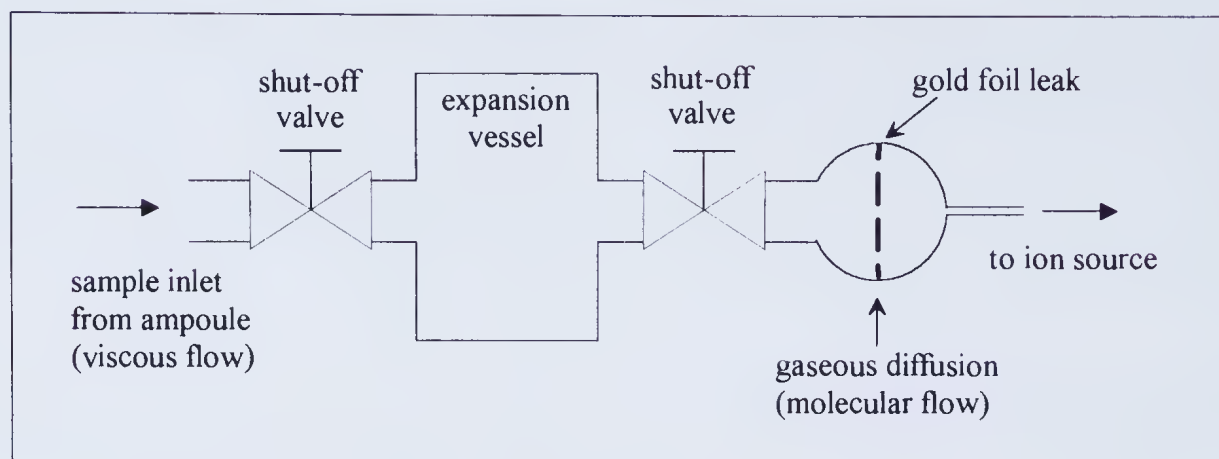


Figure 5. Inlet path of gas into ion source of gas isotope mass spectrometer.

Table 9

Theoretical and experimental values of $M(^{14}\text{N}_2)/M(^{14}\text{N}^{15}\text{N})$; uncertainties (1s) are given below the digits to which they apply.

	predicted by kinetic gas theory	experimentally observed values	difference	relative difference
$[(^{28}\text{SiF}_4)/(^{28}\text{SiF}_4)]^{0.5}$	1.00000	1.00026 0.00016		
$[(^{29}\text{SiF}_4)/(^{28}\text{SiF}_4)]^{0.5}$	1.00480	1.00469 20	0.00011 20	-1.1 10^{-4}
$[(^{30}\text{SiF}_4)/(^{28}\text{SiF}_4)]^{0.5}$	1.00957	1.00911 31	0.00046 31	-4.6 10^{-4}

and also that

$$\ln \frac{I_j(t)}{I_j(t_o)} = -\beta \cdot (M^{-\Phi} \cdot t) \quad (\text{eq. 11})$$

Consequently,

$$\ln I_{i/j}(t) = \left[\frac{iM^{-\Phi}}{iM^{-\Phi} - 1} \right] \ln \frac{I_j(t)}{I_j(t_o)} + \ln I_{i/j}(t_o) \quad (\text{eq. 12})$$

and values for $(iM/iM)^{-\Phi}$ can be estimated from the slope of $\ln I_{i/j}(t)$ against $\ln I_j(t)$.

From a best fit of these experimental values for the changing ratio, experimental values for Φ can be obtained. Optimizing instrument design, vacuum conditions and measurement procedures, the experimental values from Table 9 have been observed. The gratifying agreement with gas kinetic theory values, gives direct support that the measurement process is in a better than 10^{-3} agreement with this other law of basic physics, kinetic gas theory. The measurement process is monitored for "accuracy" by the kinetic gas theory, which gives it an additional feature for being qualified as "primary method of measurement".

Conclusions

Measurements of ratios of isotope amounts (isotopic measurements) are revealed to be of great fundamental importance not only because of their inherent potential for very small uncertainties but also for their measurement potential directly in SI units. They are fully under-

stood and are corroborated by the fundamental constants network at the $3 \cdot 10^{-5}$ combined relative uncertainty level. The measurement process itself seems to conform with kinetic gas theory at the 10^{-3} combined relative uncertainty level or better. When combined with isotope dilution, they offer the potential of opening a new route for establishing traceability of amount measurements to (a realization of) the mole, perhaps one could say, to the Avogadro constant.

Acknowledgements: A number of persons contributed substantially to the work presented and their contribution is warmly acknowledged; S Valkiers, T Murphy, S Peiser, G Lenaers, H Ku, P Hansen and D Vendelbo. I would also like to warmly acknowledge the painstaking re-editing work of H Kerslake for typing text and tables, and H Koekenberg for preparing figures.

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Atomic weights: From a constant of nature to natural variations

N E Holden

High Flux Beam Reactor, Brookhaven National Laboratory, Upton NY USA 11973

Abstract

The concept of Atomic Weight of an element as a constant of nature has played a key role in science for almost two hundred years. Two centuries ago, it helped provide credence to the atomic theory of matter. One hundred fifty years ago, the periodicity in the properties of various elements as a function of their atomic weight helped lead to the discovery of the Periodic Table and the classification of the chemical elements. Early in this present century this constant of nature concept was shaken when elements were found, which had different atomic weight values as well as different radioactive properties but they had the same chemical properties and therefore were located in the same position in the Periodic Table. To solve this problem, the concept of isotopes was born. Finally fifty years ago, the variation in nature of the composition of the stable isotopes in carbon and oxygen was found, which led to a variation in their respective atomic weights. Now mass dependent chemical reactions, nuclear reactions both natural or man-made and radioactive decay processes force us to accept the idea that atomic weights are more likely to vary in nature than they are to be constants of nature. What should we expect from atomic weights in the future?

Introduction

The world is made up of an apparently endless variety of substances; if each one is an entity in itself, the nature of matter must be forever incomprehensible. The Greeks first introduced the idea of atoms as elementary constituents of matter, but their atom was a vague general idea unattached to any specific facts or processes. John Dalton introduced his atomic theory and his table of atomic weights at the start of the 19th century. The Periodic Table was constructed using the periodicity of the chemical properties of elements in the ascending order of the atomic weights of these elements. As a result, the world was now made up of a moderate number of different real substances related in a single system and the nature of matter became comprehensible, but why did it take almost seventy years from the inception of the atomic weight concept to the publication of the Periodic Table?

In the first decade of the twentieth century, new substances were being discovered, almost daily, which had similar chemical properties to existing elements but with different atomic weight values. Bewildered scientists could not decide where to place these new discoveries in the Periodic Table. Did this invalidate the concept of atomic weights as a useful, chemical tool?

Treating the variation in the lead atomic weight as a special case, atomic weights were still considered to be constants of nature into the latter half of this century. Has this view changed? Is the atomic weight concept still useful today? We will investigate these questions in detail below.

Prehistory

The ancient Greeks first developed the idea 2500 years ago that matter was composed of atoms (Greek: indivisible). They taught that all matter was composed of four elements; fire, water, air and earth (Holden 1984). The 16th century alchemist Paracelsus added to those elements sulphur, salt and mercury.

In the seventeenth century, the Irishman Robert Boyle denied both the Greek notion that the basic elements were fire, water, air and earth and Paracelsus' salt, sulphur and mercury. He developed chemical analysis - the technique for breaking down substances into their most elemental parts. He defined an element as a material that could be identified by scientific experiment and could not be broken down into still simpler substances. This is the definition that is still in use today.

The French scientist Antoine Lavoisier revolutionized chemistry by introducing accurate weighing. He determined that a given amount of matter has a total mass as measured by a weight, which remains the same when it changes in chemical combination, whether in the solid, liquid or gaseous state. The French chemist Joseph Proust's analyses showed that a particular chemical compound always contained the same elements united in the same definite proportion by weight.

Dalton's atomic theory

The English school-teacher John Dalton tested Proust's law and noted that the same elements combined in different proportions to produce different substances. In his atomic theory, all matter was made up of particles called atoms, which were alike in everything except their weight. In chemical reactions, atoms preserved their identity and are not destroyed. When Dalton published his atomic theory, he included tables of atomic weight values (Dalton 1805).

Dalton assigned weights to atoms and expressed the relations between atoms of elements in precise numerical terms. It is possible to assign relative weights by determining the ratio in which elements reacted with each other. Having assigned hydrogen as his reference atom with atomic weight one, he calculated atomic weights by comparing weights of other atoms with that of hydrogen. When two elements combine in a compound, it is insufficient to merely determine the percentage of each element in the compound. One must also determine the valence of each element in the compound. Valence is a measure of how many atoms of one element combine with an atom of the other element, e.g. is water HO, or H_2O , or perhaps H_2O_2 ? Dalton assumed that if only one compound of two elements is known, it contains one atom of each element. This led to many difficulties in the application of his atomic theory. Equivalent weights (atomic weight/valence) were quoted rather than atomic weights.

Although his calculations were wrong, the principle was correct. However, the listing of atomic weights for some elements and fractions of atomic weights for other elements was very confusing and persisted for half a century.

The English physician, William Prout (Prout 1815) noted that Dalton's atomic weight values of elementary gases were nearly exact multiples of that of hydrogen and suggested that hydrogen was the primordial matter from which all elements are formed. For a while, it appeared that a number of atomic weight values agreed with this "Law". Testing the "Law" led to a major measurement effort of atomic weight values over the remainder of the century.

The Italian physicist Amedeo Avogadro suggested (Avogadro 1811) that all gases under the same conditions of temperature and pressure contain the same number of molecules and a molecule (Greek: a small mass) may contain more than one atom. He made a distinction between the chemical atom (smallest part of matter that can enter into combination) and physical molecule (smallest particle that can exist in a free state). This could have helped to solve the equivalent weight problem but unfortunately he used the term molecule throughout his discussion with a series of qualifying adjectives; integral, constituent and elementary. In those days, the terms atom and molecule were often used interchangeably. Some scientists understood Avogadro to imply that there could be half-atoms. This confusion caused Avogadro to be ignored for half a century.

The French physicist, Joseph Gay-Lussac determined (Gay-Lussac 1809) that gases form compounds with each other in simple (numerical) volume ratios proving that Dalton's idea of combining gases by weight alone was insufficient.

Atomic weights and the periodic table

At the Karlsruhe Congress in September 3-5, 1860, about 140 of the leading European chemists met to formulate an area of agreement among chemists regarding the nature of atoms and molecules and to reach a consensus with respect to a mutually satisfactory atomic weight scale. The Italian chemist, Stanislao Cannizzaro

presented his "Sketch of a Course in Theoretical Chemistry" (Cannizzaro 1858), where he called attention to the value of Avogadro's distinction between atoms and molecules as an organizing device for the interpretation of chemical phenomena. Lothar Meyer and Dimitri Mendeleev both attended this congress and subsequently developed periodic tables of the chemical elements based on revised atomic weight values. Mendeleev left open spaces, when no known element filled that space (Mendeleev 1869). He also predicted the properties of these unknown elements. When scandium, gallium and germanium were discovered over the next sixteen years and agreed with Mendeleev's predicted chemical properties and atomic weight, the periodic table was established and the usefulness of atomic weights was further enhanced.

As mentioned above, Prout's law spurred chemists to prodigious effort to measure atomic weights during the nineteenth century. Compare the Table from 100 years ago (Clarke 1896) with that of the International Commission for 1959 (the last one prepared on the oxygen = 16 scale). The elements not included in the 1895 Table were the noble gases and some rare earths, which had yet to be separated. Two thirds of the 1895 values listed agree to better than 1% and almost 40% agree to better than 0.1% with the 1959 values.

Radioactivity and atomic weights

At the end of the 1800s, many scientists felt that future progress was to be looked for in the measurement of variations in the sixth decimal place of fundamental constants such as the atomic weights. Roentgen's discovery (Roentgen 1895) of X-rays followed by Becquerel's radioactivity discovery (Becquerel 1896) quickly changed that viewpoint.

As radioactive materials were studied, many substances were being found with various atomic weight values. The English chemist, Frederick Soddy, showed (Soddy 1911) the chemical identity of mesothorium (^{228}Ra) and radium. In 1913, he concluded that there were chemical elements with different radioactive properties and different atomic weights but with the same chemical properties and therefore occupying the same position in the Periodic Table. He coined the word "isotope" (Greek: in the same place) to account for these radioactive species.

The study of the natural radioactive decay chains for thorium and uranium led to speculation that these parent isotopes, ^{232}Th and ^{238}U would decay into different daughter isotopes of lead, ^{208}Pb and ^{206}Pb , respectively. The lead from radioactive minerals should differ in atomic weight according to the proportion of uranium and thorium in the mineral. The atomic weight value for "common" lead (from a non-radioactive source material) was measured to be 207.2 (Baxter & Wilson 1908). Soddy & Hyman (1914) measured lead in a thorium silicate mineral to have an atomic weight value of 208.4. Richards & Lambert (1914) measured the atomic weight of lead in uranium minerals as low as 206.4.

Could stable lead be made up of a mixture of isotopes, each of a different whole number atomic weight? Was the overall atomic weight a fraction only because it

was an average? Radioactivity contributed to this problem in the case of lead, but what about the case of non-radioactive elements?

J J Thomson discovered the electron, which was found to be over a thousand times less massive than even the lightest atom. He then studied the rare gas neon in 1912 by sending a stream of cathode ray electrons through the neon gas. These cathode ray electrons knocked some electrons off of neon atoms, which left these neon atoms with a positive electric charge, so-called neon ions. In the combined presence of a magnet and an electric field, the neon ions move in a curved path. If all neon ions had the same mass, all would follow the same curve. If some were more massive than others, the more massive ones would curve less. Thomson detected the neon ions at the end of their path on a photographic plate. He measured the darkening of the plate and found two locations which from the amount of curvature had to be ^{20}Ne and ^{22}Ne . The intensity of darkening indicated amounts of 90% and 10%, respectively. The overall atomic weight of neon, 20.2, was the average atomic weight of these two isotopes. Thomson's instrument, the fore-runner of the "mass spectrometer", was the first one capable of separating isotopes.

The Englishman, Francis W Aston used a mass spectrograph (Aston 1929) to analyze a sample of lead showing lines on the photographic plate at masses 206, 207 and 208 with intensities of 100, 10.4 and 4.5, respectively. Aston concluded that mass 207 must be the end product of the actinium radioactive decay series and was probably derived from an isotope of uranium and it would have a mass of 235. ^{235}U was found six years later.

Lead has four isotopes, of which only ^{204}Pb is not produced from radioactive decay. The American physicist, Alfred Nier used this peak as a reference in a mass spectrometer. He showed (Nier 1938) that the relative abundances of the lead isotopes varied widely even in common lead, which had a nearly constant atomic weight value. Nier's work on lead's isotopic composition was also useful for dating purposes and the measurement of geological time (Nier 1939).

There is no longer a case of an element like lead having varying isotopic compositions but a constant atomic weight because atomic weights are now determined by isotope mass spectrometry almost exclusively (De Bièvre 1973).

The atomic weight scale

The atomic weight scale $H = 1$ was originally conceived used by Dalton and was used for 100 years. The Commission on Atomic Weights changed to the $O = 16$ scale with its 1906 report (Holden 1984). Both hydrogen and oxygen were thought to not have isotopes. The discovery of oxygen isotopes in infrared spectra (Giauque & Johnson 1929a,b) led to a situation where the chemists scale of $O = 16$ differed from the physicists scale of $^{16}\text{O} = 16$. When a variation was found in oxygen's atomic weight in water versus air (Dole 1935), this implied a variation in the isotopic composition of oxygen and the two scales took on a small but variable difference. In

April 1957 at a hotel bar in Amsterdam, Nier suggested (Holden 1984) that the $^{12}\text{C} = 12$ scale be adopted because of carbon's use as a secondary standard in mass spectrometry. Physicists' approval was obtained, and in 1961 the atomic weights were officially given on the $^{12}\text{C} = 12$ scale for the first time (Cameron & Wichers 1962).

Variations

Although the atomic weight scale difficulty had been solved, another problem began to plague the Atomic Weights Commission. Nier & Gulbransen (1939) had made measurements on carbon which showed 5% variation in the isotopic composition. The atomic weight would vary depending on the source of the material studied. Although the lead atomic weight variation could be ignored, the variation in carbon and in oxygen, mentioned earlier, made it apparent that atomic weights were not constants of nature. Variations in many light elements have since been found as well as variations due to radioactive decay in a parent affecting the isotopic composition and atomic weight of the daughter. For 30 years, restrictions on quoted atomic weight values have acknowledged these variations.

Speculations and conclusions

After the problem with lead, Richards had speculated on whether the supposed constant atomic weight magnitudes in chemistry were really variable? If so, how much effort should be expended in determining atomic weight values? One must determine the detailed variation to understand causes of the variation. Evaluations of isotopic compositions have been added to the responsibility of the Atomic Weights Commission. Examples will illustrate some of the interesting problems that are now addressed.

Reference has already been made to the use of the isotopic variations in uranium dating of geological times. There are a host of other dating methods which involve selecting a decay system with the same magnitude of half-life as the age of the material to be studied.

Boron is an element with a large probability for reacting with neutrons, so boron was used as a standard for measuring other elements. However, these measurements at different laboratories gave dissimilar results, which was traced to the use of boron samples with different atomic weights and isotopic composition at these labs. This variation now restricts the accuracy with which the atomic weight of boron can be quoted.

In 1972, uranium ore from the Oklo mine in Gabon, West Africa was shown to contain too low an amount of ^{235}U compared to normal uranium. Additional analyses indicated that the ^{235}U had been burned up in a natural fission chain reaction under the ground about 2 billion years ago. The isotopic composition of various chemical elements was not consistent with normal samples of these elements but was consistent with the yield of the various isotopes as produced in the fission process (Ruffenach *et al.* 1980). These variations are now made note of when reporting the standard atomic weight values.

Table I.

Comparison of 1895 & 1959 atomic weight values based on oxygen = 16.000 scale

Element	1895	1959	Element	1895	1959	Element	1895	1959
Actinium	Unknown	(227)	Glucinum	9.08	(Beryllium)	Praseodymium	143.5	140.92
Aluminum	27.11	26.98	Gold	197.24	197.0	Promethium	Artificial	(145)
Americium	Artificial	(243)	Hafnium	Unknown	178.50	Protactinium	Unknown	(231)
Antimony	120.43	121.76	Helium	Uncertain	4.003	Radium	Unknown	(226)
Argon	Uncertain	39.944	Holmium	Unlisted	164.94	Radon	Unknown	(222)
Arsenic	75.09	74.92	Hydrogen	1.008	1.0080	Rhenium	Unknown	186.22
Astatine	Unknown	(210)	Indium	113.7	114.82	Rhodium	103.01	102.91
Barium	137.43	137.36	Iodine	126.85	126.91	Rubidium	85.43	85.48
Berkelium	Artificial	(249)	Iridium	193.12	192.2	Ruthenium	101.68	101.1
Beryllium	(Glucinum)	9.013	Iron	56.02	55.85	Samarium	150.0	150.35
Bismuth	208.11	208.99	Krypton	Unknown	83.80	Scandium	44.0	44.96
Boron	10.95	10.82	Lanthanum	138.6	138.92	Selenium	79.0	78.96
Bromine	79.95	79.916	Lead	206.92	207.21	Silicon	28.40	28.09
Cadmium	111.93	112.41	Lithium	7.03	6.940	Silver	107.92	107.873
Calcium	40.08	40.08	Lutetium	Unknown	174.99	Sodium	23.05	22.991
Californium	Artificial	(251)	Magnesium	24.29	24.32	Strontium	87.61	87.63
Carbon	12.01	12.011	Manganese	54.99	54.94	Sulfur	32.07	32.066
Cerium	140.2	140.13	Mendelevium	Artificial	(256)	Tantalum	182.6	180.95
Cesium	132.89	132.91	Mercury	200.0	200.61	Technetium	Artificial	(99)
Chlorine	35.45	35.457	Molybdenum	95.98	95.95	Tellurium	127.07	127.61
Chromium	52.14	52.01	Neodymium	140.5	144.27	Terbium	160.0	158.93
Cobalt	58.93	58.94	Neon	Unknown	20.183	Thallium	204.15	204.39
Columbium	94.0	(Niobium)	Neptunium	Artificial	(237)	Thorium	232.63	(232)
Copper	63.60	63.54	Nickel	58.69	58.71	Thulium	170.7	168.94
Curium	Artificial	(247)	Niobium	(Columbium)	92.91	Tin	119.05	118.70
Dysprosium	Unlisted	162.51	Nitrogen	14.04	14.008	Titanium	48.15	47.90
Einsteinium	Artificial	(254)	Nobelium	Artificial	(254)	Tungsten	184.84	183.86
Erbium	166.3	167.27	Osmium	190.99	190.2	Uranium	239.59	238.07
Europium	Unknown	152.0	Oxygen	16.000	16.000	Vanadium	51.38	50.95
Fermium	Artificial	(253)	Palladium	106.36	106.4	Xenon	Unknown	131.30
Fluorine	19.03	19.00	Phosphorus	31.02	30.975	Ytterbium	173.0	173.04
Francium	Unknown	(223)	Platinum	194.89	195.09	Yttrium	88.95	88.91
Gadolinium	156.1	157.26	Plutonium	Artificial	(242)	Zinc	65.41	65.38
Gallium	69.0	69.72	Polonium	Unknown	(210)	Zirconium	90.6	91.22
Germanium	72.3	72.60	Potassium	39.11	39.100			

Many elements are produced which are enriched in less abundant isotopes and are used as tracers in medical diagnoses of processes in humans when use of radioactive tracers is not appropriate, e.g. in children and pregnant women. Note should be made that standard atomic weight values may not apply to these "doctored" elements.

Carbon has two stable isotopes, ^{12}C and ^{13}C . The study of diet uses the ^{13}C abundance variation in the two major photosynthetic pathways; C_3 plants - wheat, rice, beans and nuts, are depleted in ^{13}C relative to atmospheric CO_2 and as compared to C_4 plants, such as corn and sugar cane, which come from warm environments. Similarly, nitrogen has two stable isotopes, ^{14}N and ^{15}N . The abundance of ^{15}N is enhanced in marine plants relative to land plants. This can be used to study changes in diet, when our ancestors moved from a hunting society to one dependent on marine life and on to the cultivation of plants.

Earth and planetary science studies the isotopic anomalies (Shima 1989; Shima & Ebihara 1989) in meteorites and moon rocks to understand differences in processes of origin of the solar system $1\text{--}1.5 \times 10^{10}$ years ago compared to the earth some 4 or 5×10^9 years ago.

We have seen how the concept of atomic weights has evolved over the past two centuries. There was much interest when atomic weights were considered constants of nature and even more interest now that they are known to be variable. The demonstrated uses (de Laeter 1988, 1990; de Laeter *et al.* 1992) of the underlying fundamental isotopic compositions exceed the few examples cited and I anticipate even more extensive uses of isotopes will be found in the future.

Acknowledgements: This paper is dedicated to Professor J de Laeter on his retirement as Deputy Vice Chancellor, Curtin University. This work was performed under the auspices of the US Department of Energy (Contract DE-AC02-76CH00016).

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Ion optical design for mass spectrometers

S W J Clement

Research School of Earth Sciences, Australian National University, Canberra ACT 6001

Abstract

The efficient operation of mass spectrometers, since the development of the earliest instruments, has depended on the analogy between the optics of light and the 'focussing' effect of various electromagnetic fields acting on charged particles. Without the first order refocussing of the simple magnetic sector field, even modest mass resolution would be achieved only by extreme collimation of the ion beam and at a heavy penalty in sensitivity. Over the years, the increasing level of sophistication in the theoretical analysis of mass spectrometers as ion optical systems has led to real improvements in the operational performance of the instruments as analytical tools. It is now common to find mass spectrometers with non-normal incidence to the magnet, curved field boundaries, contoured magnet pole-faces, and spherical or toroidal electrostatic analysers. These and other devices are now being used to provide first and higher order focussing in both the dispersive and non-dispersive planes.

Further insight into the operation of mass spectrometers has been gained by the application of the phase space concepts originally introduced in the beam transport field of nuclear physics. The ideas of beam emittance and instrument acceptance are now widely understood and their correct matching is seen as fundamental to the ion optical design of a new instrument. Liouville's Theorem has also emphasised the relationship between mass resolution, ion transmission efficiency and instrument parameters such as accelerating potential and magnet radius.



Sensitive High Resolution Ion Micro-Probe (SHRIMP) at Curtin University in the Isotope Science Research Centre. See Compston (1996, in this issue) for the development of SHRIMP.

Clean laboratories: Past, present and future

J R Moody

Chemical Science and Technology Laboratory, National Institute for Standards and Technology,
Gaithersburg MD USA 20899.

Abstract

Clean chemistry laboratories have become rather ubiquitous for the ultra-trace analysis of elements, especially among those laboratories that work in the area of isotope geochemistry. The need for the control of analytical blanks has almost always been appreciated, but became the primary concern of analysts as new measurement technology opened the door to elemental measurements on amounts of substance equal to a nanogram or less. Since common laboratory environments expose samples to a contaminant deposition of up to one microgram in a 24 hour period, cleaner environments were recognized as necessary. In the 1960s, a number of laboratories applied clean air technology from the space and electronics industries to the chemical laboratory.

The results from these pioneering efforts and the need to accurately measure elemental and isotopic compositions on the Apollo lunar samples led the National Bureau of Standards to build several complete clean air laboratories dedicated to sample preparation wet chemistry. These laboratories were simple but effective in design and have been extensively copied by other laboratories. By the early 1980s, the issue of air quality (the Class of the clean air) was beginning to be recognized by many as less important than the other issue in clean laboratory design. That is, contamination reduction may depend as much or more on keeping gross quantities of analyte elements out of the laboratory and preventing the formation of undesirable corrosion products. This was not news for the geochemistry community, but by the 1980s it had become a mainstream problem for trace element analytical chemistry, primarily because of the new focus of analytical chemistry on environmental measurements. The question now is where does clean laboratory design go to exact further improvements in laboratory performance. Part of the answer may lie in examining other trends in analytical chemistry and projecting how a clean laboratory might accommodate them.

Introduction

Clean chemistry laboratories for the ultra-trace analysis of elements have become common, especially among those laboratories that work in the area of isotope geochemistry. However, back in the 1960s most analysts were still working in open laboratories. Most wet analysis was performed in glass apparatus using commercially available reagents equivalent to the American Chemical Society's (ACS) Reagent Grade. Elemental blanks from the reagents and apparatus alone amounted to more than a few micrograms. Some geologists were fortunate enough to be working with isotopes of elements of relatively low abundance. Few analytical chemists considered the environmental blank contribution to be a limiting factor in their analyses. Fortunately, isotope geologists were among the first to look for ways to lower the analytical blank since they were often limited in sample size or they were analyzing isotopic compositions at very low elemental concentrations. At the US National Bureau of Standards (NBS; now National Institute for Standards and Technology, NIST) in the late 1960s, scientists were measuring the elemental deposition from the air in the laboratories and they could easily find significant contaminations of 0.1-0.5 μg per day for elements like lead.

As the emphasis in inorganic analytical chemistry turned more toward trace analysis, analysts in many laboratories were discovering contamination problems in their measurements. The isotope geology laboratories and semiconductor electronics laboratories were the first to take positive steps to minimize contamination. Zief & Mitchell's (1976) book on contamination control was a real turning point in trace analysis for the general analytical community; it detailed procedures that had been in use at select laboratories for a number of years. A paper by Patterson & Settle (1976) represents another milestone in approaches to contamination control. Although both may be difficult to obtain now, they are superlative references since relatively little has changed in clean lab procedures from the principles presented by these authors. The NBS laboratories have published a guide to clean laboratory construction (Moody 1982) that has been widely used by many laboratories around the world. Although the basic design is still valid, we will try to project what the analytical clean laboratory might look like in ten years.

Historical Approaches to Contamination Control

The simplest approach to the control of contamination from laboratory air was to enclose the experiment inside a plastic box. Contamination was thus reduced to the amount of contamination contained within the box.

A more sophisticated approach was to use a filtered supply of nitrogen or another inert gas to flush the sample containment box and to keep it under a slight positive pressure. This prevented the influx of contaminants from outside of the box. Gloved ports were used for access to the sample. The major problem with this approach was the inconvenience involved. Dissolutions inside the box could be tricky and some sort of fume eradicator (a canopy to siphon off fumes) was necessary.

In the late 1960s and early 1970s, a few laboratories started to explore the use of clean air technology for application to the laboratory. The object was to overcome some of the difficulties of working in a closed system and still preserve the contamination control aspects in a new configuration. At this time, clean air was already extensively used in electronics manufacturing, medicine, and aerospace. The HEPA (High Efficiency Particulate) filters used were typically 99.97% efficient at 0.5 micrometer particle sizes. In an ordinary laboratory, a few filters could provide a huge improvement in the overall laboratory air quality and relatively high air quality in the designated clean bench area. Several of these designs were published (Patterson & Settle 1976; Zeif & Nesher 1974; Mitchell 1973). All required relatively stringent laboratory access procedures to keep the laboratory environment clean. None would meet strict air quality definitions but all were certainly useful.

An example of such a laboratory was the clean laboratory at the University of Ghent, Belgium. Designed by Versieck and Cornelis, the laboratory was used for their pioneering work on the analysis of trace elements in biological and clinical samples. Mitchell (1973) at the Bell Telephone Laboratories in the USA was another early pioneer in the development of a working clean laboratory for chemical operations. Typical clean air flow amounted to the equivalent of one room air change in a period of one to three minutes. NBS purchased a commercial clean room for chemical analysis in 1968 with much higher air flows, although nothing else in the laboratory was optimised for chemistry. This laboratory did not perform well for chemical applications. The greatest change in the approach to chemistry clean laboratory design probably occurred in 1971 at NBS when the inorganic mass spectrometry group built a new clean laboratory specifically for the analysis of the Apollo lunar rock samples. The adoption by NBS of a new approach to clean laboratory design would not have happened without the prior four years experience with a commercial clean room and the results observed in the efforts of other trace analysts.

The resulting NBS clean laboratory and its successor were described in detail by Moody (1982). These laboratories were simple but effective in design and have been extensively copied by other laboratories. By the early 1980s, the issue of air quality (the Class or cleanliness of the clean air) was beginning to be recognized by many as less important than other issues in clean laboratory design. That is, contamination reduction in a clean laboratory may depend as much or more on keeping gross quantities of analyte elements out of the laboratory and preventing the formation of undesirable corrosion products. This was not news for the geochemistry community, but, by the 1980s contamination and its prevention

had become a mainstream problem for trace element analytical chemistry, primarily because of the new focus of analytical chemistry on environmental measurements.

Present Day Clean Laboratory Design

At the present time, the International Standards Organisation (ISO) is preparing a new standard for the measurement and classification of clean air and other standards are also undergoing some revisions. At this time it is premature to quote new draft technical standards. These standards will harmonise nomenclature and clarify classifications of laboratories but the standards do not address real laboratory performance for chemistry applications. Technical standards aside, the actual quality of the HEPA filter has been improved greatly over the last twenty years allowing the air quality in the laboratory to be improved by a factor of one hundred or more over what was achievable in the early 1970s. The design of the filter has also improved, allowing the trace analyst to specify both a more efficient filter and metal-free filter body. It would be a mistake, however, to assume that improvements in the clean laboratory air quality have led to a corresponding improvement in the analytical blank.

Most of the earliest clean rooms for chemistry employed horizontal air flow. They also had a relatively small HEPA filter area relative to the volume or area of the laboratory. The NBS (NIST) design adopted a modified vertical flow industrial design. This approach required a total filter area, volume of air flow, and shortness of residence time for air in the clean laboratory that was significantly different compared to contemporary chemistry laboratories employing clean air. While the problems in chemistry applications are different from industry, the NBS (NIST) design shared more than a few common elements with industrial design. A deliberate attempt was made to keep the entire laboratory involved in the air circulation pattern to both reduce the residence time of the air in the laboratory and to effectively flush particles from the room that were produced by chemical processes.

Fume hoods were designed to handle perchloric acid in a laminar flow clean air environment. Whereas most industrial clean rooms operate at almost 100% recycling of the clean air, the NBS laboratory exhausted 35% or more of the total clean air through the fume hoods, thus reducing the recycled air to less than 65%. This meant that a high proportion of dirty make up air had to be introduced to the room to maintain the pressurisation of the laboratory. This created another break with traditional clean room design. With near 100% recycling, environmental controls (temperature and humidity) have to be built into the clean air handling system. It was not unusual to see facilities that devoted as much space to the installation of technical equipment as was devoted to the clean air space. This was expensive and wasted valuable laboratory space.

Because the NBS laboratories were retrofitted into existing spaces, all available space was at a premium. Consequently NBS turned to a system of modular clean air units that could be incorporated into the ceilings of existing laboratories. Since fume exhaust was to be about 35% of the total room air, the make up air normally

provided to the laboratory could handle all of the air conditioning and heating needed without having to modify any of the existing building air handling systems. The design was significantly cheaper than other approaches and over the years it has performed as well as or better than more conventional clean room designs. The entire sample handling areas have very high quality vertical laminar flow clean air which effectively isolates the samples from the analyst(s). All aspects of sample handling, dissolution, and separation were accommodated within the clean laboratory to eliminate the necessity of going in or out of the laboratory to perform another sample preparation step. The result of these and other factors such as ultra-purified reagents led to a substantial improvement (factor of 10 to 1000 or better) in the analytical blank in our laboratory and in others with similar operating conditions. Literally hundreds of copies of the laboratory have been constructed over the years with little change in the basic design.

The NBS (NIST) designers tried to provide the maximum performance for the least cost. However, despite the enormous improvements in measured air quality in the newest NIST clean laboratory, there has been little if any improvement in the analytical blanks attributable to the clean laboratory. Where blank reductions have been achieved, the results were through improvements in the analytical method, separations, or choice of reagents employed. The clean laboratory blanks seem to have been constant. One reason for this is that our laboratories are not totally metal free, leading to contamination by secondary causes such as touching or handling of artifacts in the laboratory that ultimately transfer to the samples when handled. Another reason is that to keep the laboratory as fully utilized as possible and to make its use attractive to staff, personnel hygiene restrictions have been relatively relaxed. Thus, improvements in procedures could be used to improve the laboratory performance even further. Nevertheless, the clean laboratory itself does not seem to be a major contributor to analytical blanks. Other factors such as ion exchange resins, reagents, and labware are larger contributors to the blank problem.

Recently, a few laboratories have attacked this one weakness of the NBS/NIST design clean laboratory. Two laboratories that have done an outstanding job of reducing secondary contamination sources (contamination not transmitted by the HEPA filter) are Boutron's laboratory in France (Boutron 1990) and De Bièvre's laboratory at the Institute for Reference Materials and Measurements (IRMM) in Belgium. Both laboratories have made extensive use of plastics to replace other materials of construction in the laboratory. The IRMM laboratory in Belgium is probably the ultimate achievement for the present clean air technology and laboratory design. Since the NBS or NIST designs are widely known and published, it may be more useful to examine how IRMM improved on the last NIST design. As with all discussions of clean laboratory design, the reader must judge the best design or feature for their application.

Planning for the IRMM facility began with NBS assistance in 1985 and continued for several years before a final design was accepted. All commercial clean rooms employ the principle of shelling or compartmentalizing clean operations inside of progressively cleaner environ-

ments. Patterson and Settle's (1976) chemical and sampling operations were based on the same principle, and these have been proven to be effective and necessary in instances of extremely low analyte concentration. Where the NBS laboratory employed zero or minimal progression into the cleanest environment, the IRMM facility has four distinct air quality zones starting with the complete isolation of the clean laboratory building from the adjacent mass spectrometry facilities. The laboratory facilities are classified as Class 1000, Class 100, and Class 10. Actual performance is better than specified.

The entire clean laboratory building at IRMM is physically isolated and supplied with HEPA filtered clean air. Although our experience at NIST has indicated that the HEPA filters may last for four to five years, there is little doubt that the relatively poorly filtered air supply to the NIST laboratories shortens the useful lifetime of the HEPA filters. The major justification for HEPA filtering for the entire building air supply at IRMM was that it would extend the clean laboratory HEPA filter life and also provide a high quality air supply for the building to further reduce the chance of contamination in the laboratories. Initially, this approach is expensive, but the redundant HEPA filter chambers used for the building air conditioning mean that the filters may be serviced or replaced with no interruption of service to the laboratories.

In addition to the highest level of air quality, all of the laboratory components are made of plastic or of materials that are fully protected from corrosion caused by wet chemical processes. The restrictions on use by laboratory personnel together with the modular design and metal free constructions go as far as seems possible towards reducing secondary contamination from the laboratory and from the chemists. The IRMM laboratory design probably represents the final stage of clean room evolution using conventional laboratory approaches. The question now is where does clean laboratory design go to extract further improvements in laboratory performance. Part of the answer may lie in examining other trends in analytical chemistry and projecting how a clean laboratory might accommodate them.

The Clean Laboratory of the Future

The largest consumer of clean room apparatus is the electronics industry. All of the clean laboratories in the world constitute an almost imperceptible fraction of the clean rooms constructed for the electronics industry each year. One may start with the premise that the only equipment that one can buy is the equipment that is manufactured for this industry. The medical industry is another large consumer of clean room equipment, but their equipment is still derived from the semiconductor market. One disturbing trend for analysts is a current trend in the semiconductor industry. With the ever decreasing size of microelectronic circuitry on chips, the demand for better air quality (ULPA filters, for instance) is leading to some manufacturing changes. In the 1970s we were careful to move from steel filter frames to aluminium frames and then to wood frames (metal-free) for the HEPA filters. With the demand for low particle counts, the wood frame is being phased out to accommodate the use of metal filter frames. Metals do not

contract or expand with temperature or humidity as much as wood. The reality is that we will have to adapt to the use of metal frames again over the next five years or so. This will create some problems in making these filters suitable for use in a trace metals laboratory. Particle counts will be lower, but much more care will be needed to protect the HEPA filter from corrosion.

The other trend that one may see in the electronics industry is a rapid adoption of automation to remove the human operator from the process. This in turn is leading to changes in equipment design and philosophy. In analytical chemistry, you may also see this trend with the rapid adoption of laboratory automation. The motivation for the laboratory manager may be to reduce laboratory costs more than to improve performance. Nevertheless, it is probably safe to assume that automation will become a majority factor in laboratories of the near future. Wet chemists with the knowledge to perform many laboratory operations are also disappearing.

Based upon these trends, this author speculates that the laboratory of the future will be built around automated apparatus. Further, it is likely that the most efficient way to do this is to adopt the semiconductor industry developed "mini-environment." The mini-environment is a fully self contained clean process with clean air, robotics, wet benches, *etc.* built into a closed chamber. These may be grouped and ganged together to perform sequential operations. They provide much better air quality with total isolation from the clean room in which the mini-environment is located. Ventilation and heating requirements may be greatly reduced since the environment provided is what the process needs, not what humans require. Chemists would have relatively little direct contact with a sample in this kind of clean room. Finally, there is one other advantage to the mini-environment approach. The cost is much less than

would be needed to achieve similar process performance by conventional means.

If building a clean laboratory of about 100 m² today, one might spend well in excess of \$(US)2,000,000. The cost for a clean room of similar performance utilizing mini-environments would be much less than half of that. Operating costs could be similarly cheaper for the minienvironment. Such a laboratory could not be built today since the automated laboratory equipment does not yet exist for many analytical operations. Finally, the analytical chemical process itself may be significantly improved with a more consistently clean operation without human intervention. No other large improvements in clean laboratory performance seem likely with the present design approaches.

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Meteorites recovered from Australia

A W R Bevan

Department of Earth and Planetary Sciences, Western Australian Museum, Francis Street, Perth 6000

Abstract

Meteorites are our only tangible source of information on the earliest history of the Solar System. Over the last ten years the number of meteorites described from Australia has doubled, and this has stimulated many new lines of enquiry. To date, fragments from a total of 474 distinct and authenticated meteorites have been recovered in Australia. The material, including 13 meteorites observed to fall, comprises 389 stones (21 achondrites, 366 chondrites and 2 unclassified stones), 71 irons, 13 stony-irons and one meteorite of unknown class. Two hundred and fifty-seven distinct meteorites are currently known from Western Australia, 123 from South Australia, 48 from New South Wales, 20 from Queensland, 12 from the Northern Territory, 10 from Victoria and 4 from Tasmania. Discoveries include the first lunar meteorite (a fragment of the Moon), Calalong Creek, found outside of Antarctica. Five meteorites (Veevers [iron], Wolf Creek [iron], Henbury [iron], Boxhole [iron], and Dalgara [mesosiderite stony-iron]) are associated with craters. Another eighteen impact structures (lacking meteorites) are known in Australia and the country has one of the world's best preserved impact cratering records stretching back more than 500 million years. Most meteorites in Australia have been found in the Nullarbor Region, which for climatic and geological reasons is one of the most prolific areas of the world for meteorite recoveries outside of Antarctica. Since 1971, several thousand specimens of an as yet unknown total number of distinct meteorites have been recovered from the Nullarbor, including many rare types. ^{14}C terrestrial ages of Nullarbor meteorites combined with population statistics are providing important information about the number of meteorites falling with time. Moreover, weathering studies of ancient stony meteorite finds, and the stable isotopic composition of carbonate contamination derived from the Nullarbor limestones is yielding palaeoclimatic information for that region of Australia over the last 30,000 years.

Introduction

Meteorites are an unique source of information about the earliest history of the Solar System. Mostly fragments broken from small planetary bodies, called asteroids, in solar orbits between Mars and Jupiter, many meteorites have remained virtually unaltered since their formation 4.55 Ga ago. Some rare types of carbonaceous meteorite contain water and complex carbon compounds, including amino acids. These rocks may be similar to the original materials from which the Earth gained the water for its oceans, the gases for the atmosphere we breathe, and the building blocks of life. However, aside from the fundamental question of the origin of life, basic research on meteorites is helping us to understand many other aspects of our natural environment and history. Research on Australian meteorites essentially started with the publication by Haidinger (1861) of a description of two masses of the Cranbourne iron meteorite found in Victoria in 1854.

On numerous occasions in the past, meteorites found in Australia have been reviewed, or listed (e.g. Cooksey 1897; Anderson 1913; Prior 1923; Hodge-Smith 1939; Prior & Hey 1953; Hey 1966; Mason 1974; Gibbons 1977; Graham *et al.* 1985; Bevan 1992a). Most recently, Bevan (1992a) provided a comprehensive review of meteorite recovery in Australia. However, since the early 1990's there has been a surge in the recovery of meteorites in Australia that has opened up many new lines of research.

Figure 1 shows the numbers of meteorites known at various times from Australia during the period 1897-1996. Mason (1974) documented a total of 184 distinct meteorites from Australia. During the period 1974-1992, data were published for 93 new Australian meteorites (Bevan 1992a). However, since the last review by Bevan (1992a), data for an additional 197 meteorites from Australia have appeared in the literature. This remarkable recovery rate is largely due to discoveries in the Western Australian and South Australian Nullarbor Region. For climatic and geological reasons, the Nullarbor Region is one of the most prolific desert areas of the world for meteorite recoveries outside of Antarctica (Bevan &

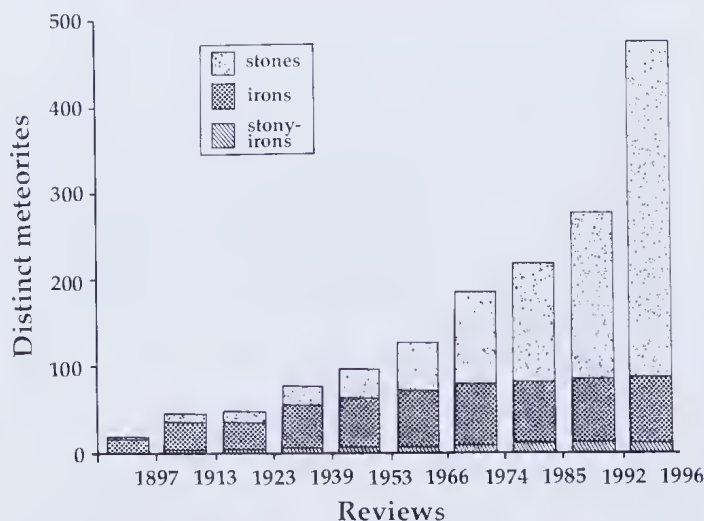


Figure 1. Cumulative histogram of meteorites known from Australia at various times during the period 1897-1996.

Binns 1989a,b,c; Bevan 1992a; Bevan & Pring 1993). Recoveries from the Nullarbor alone account for more than 50% of all meteorites currently known from Australia, and more than a thousand recently recovered, and potentially new, Nullarbor meteorite fragments remain to be described (Bevan 1992b; Koeberl *et al.* 1992).

The purpose of this paper is to review Australian meteorites, particularly those recovered since the last review by Bevan (1992a), and with special reference to the unique environment of the Nullarbor Region, to examine the climatic and physiographic factors that contribute to the recovery of meteorites in Australia.

Meteoritic materials and origin

Only a brief resumé of meteorite classification and genesis is presented here. For more detailed accounts, the reader is referred to the bibliography and references therein (*e.g.* Dodd 1981; McSween 1987).

Traditionally, meteorites have been divided into three major categories depending on the relative amounts of silicate and metallic minerals they contain. *Iron* meteorites are composed predominantly of iron-nickel metal; *stony* meteorites (often called 'stones') consist mainly of silicates, but also contain some metal and other accessory and minor mineral phases; and *stony-irons* comprise metal and silicates in roughly equal amounts. About 95% of modern observed meteorite falls are *stones*, around 4% are *irons* and only 1% are *stony-irons*. This simple classification scheme, however, conceals the diversity of materials that have fallen to Earth, and modern research has delineated numerous distinct groups and sub-types of meteorites.

Stones

Of the two main groups of stony meteorites recognised, the *chondrites* are the most numerous, accounting for 87% of all meteorites observed to fall. Chondrites contain millimetre-sized beads of stony minerals, called *chondrules*, from which the name of the group originates (Fig 2). Chondrules are unknown in any rocks from Earth and for more than a century arguments have continued over how these enigmatic objects might have formed. While there is still no consensus on

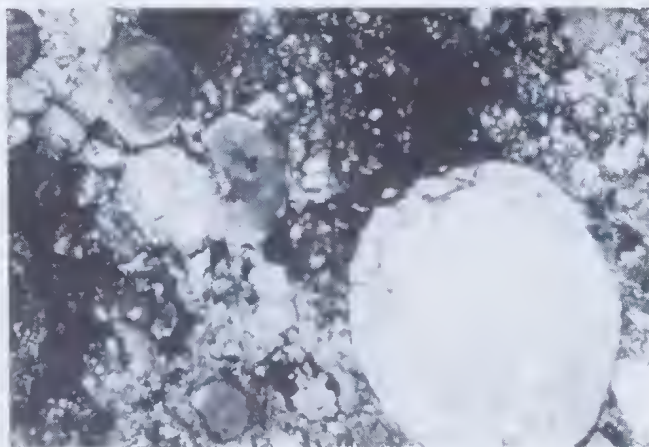


Figure 2. Photomicrograph of the Forrest Lakes LL5 ordinary chondrite showing numerous rounded chondrules.

the mechanism by which chondrules were generated, most researchers agree that chondrules were among the earliest materials to have formed in the Solar System. An understanding of the origin of chondrules, and subsequent chondrites, is fundamental to our understanding of how materials (and ultimately planets) formed in the infant Solar System. Chemical variations between chondritic meteorites define a number of distinct groups.

The largest group, collectively known as the *ordinary chondrites*, accounts for more than half of all known meteorites (observed falls + chance finds) (*e.g.* see Fig 3). Although 75% of their bulk is made up of silicate minerals, ordinary chondrites contain substantial amounts of iron both in the form of silicates and as metal and iron-sulphide. Two other rarer groups of chondrite, *enstatite* and *carbonaceous chondrites*, represent extremes in composition. The enstatite chondrites are rich in metal and sulphide, but the main silicate mineral they contain (enstatite) is a pure magnesium-silicate containing no iron. In contrast, carbonaceous chondrites contain little or no metallic iron, but their silicate minerals are mostly iron-rich.

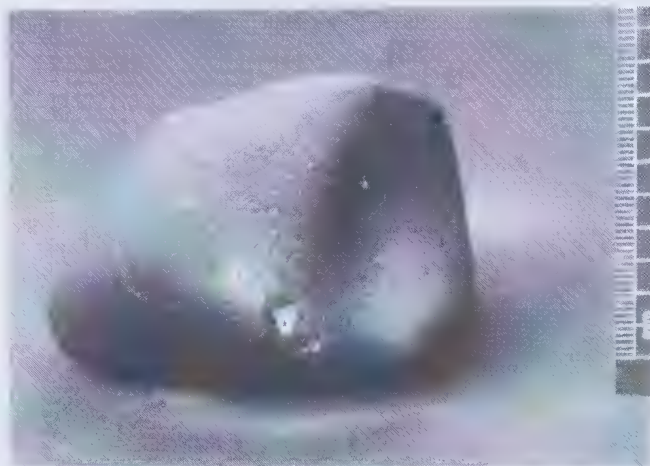


Figure 3. Mass of the ordinary chondritic (H5) meteorite that fell on Binningup beach, Western Australia, at 10:10 am on 30 September, 1984.

Carbonaceous chondrites are among the most important and intriguing classes of meteorites. Sometimes rich in complex carbon compounds such as amino and fatty acids, carbonaceous chondrites can also contain appreciable amounts of water (up to 20%), and water-bearing minerals that formed by the hydrothermal alteration of other minerals. A rare type of carbonaceous chondrite [CI], named for the type meteorite Ivuna (that fell in Tanzania), of which only a few are known, is composed almost entirely of minerals that formed at low temperatures. Significantly, some of these meteorites have chemistries that closely match the Sun's, and are our best samples of 'average' Solar System material. The majority of meteorites are believed to be fragmental debris from the collision of asteroids, but there is astronomical evidence suggesting that some carbonaceous chondrites may have had a cometary origin.

The *achondrites* make up around 8% of modern meteorite falls. So-called because they lack chondrules, achondrites generally have textures showing that they formed in similar ways to some of the igneous and volcanic rocks on Earth. Although most achondrites are

asteroidal in origin, twelve are fragments of the Moon. These "lunar" meteorites were probably ejected from the Moon by large, low-angle impacts. We are able to recognise lunar meteorites by comparison with the reference collection of lunar rocks returned by the Apollo space missions and knowledge of the Moon's chemistry. Another twelve achondritic meteorites are planetary in origin and may be fragments of Mars (e.g. see Gladman *et al.* 1996 and references therein). Unlike meteorites of asteroidal origin, these meteorites crystallized only 200-1300 million years ago and must have come from a large, planetary-sized body that remained hot for much longer than the asteroids.

Irons

The chemical make-up of irons suggests that most solidified from molten accumulations of metal that could only have formed deep in the interiors of a number of small asteroids (Fig 4). Irons often consist of two iron-nickel minerals arranged in a regular trellis-work structure of interlocking crystal plates. When cut and polished surfaces of some irons are treated with acid, this structure, called a Widmanstätten pattern is revealed (Fig 5). Widmanstätten structures formed as the result of extremely slow cooling of hot metal in the solid state. Cooling rate calculations indicate that many irons are fragments of the cores of small asteroidal bodies ranging up to a few hundred kilometres in diameter. Like achondrites, most iron meteorites tell us that some bodies smaller than planets in the early Solar System melted and differentiated, separating metal from silicate to form 'cores' and 'crusts' like the Earth's. Other iron meteorites were never completely melted and some contain inclusions of silicate. The modern classification of irons is based on chemistry, notably the abundance of Ni, Ga, Ge and Ir that they contain.



Figure 4. Main mass, weighing 480 kg, of the Haig (group IIIAB) iron meteorite found on the Nullarbor Plain by Mr A J Carlisle in 1951 (photograph by D. Elford).



Figure 5. Cut, polished and acid treated slice of the Haig iron meteorite showing the Widmanstätten pattern characteristic of this group of irons (sawn edge measures 8 cm).

Stony-irons

Stony-irons are by far the rarest of the main categories of meteorites. Two main groups of stony-irons are recognised. Meteorites of the largest group, the *pallasites*, are composed of crystals of olivine set in metallic iron-nickel. Members of the other major group of stony-irons, called *mesosiderites*, are made up of mixtures of fragments of rock similar to some achondrites in composition, and nuggets and veins of iron-nickel metal. There are also several anomalous meteorites (e.g. Bencubbin) that fit structurally into the stony-iron category, although these have no relationship to the two major groups. Bencubbin is a complex mixture of metal and silicate components, including a variety of chondritic xenoliths an example of which is seen as a dark area on the cut face of the meteorite (Fig 6). Bencubbin is not related to any of the known major groups of meteorites although some components are chemically and isotopically

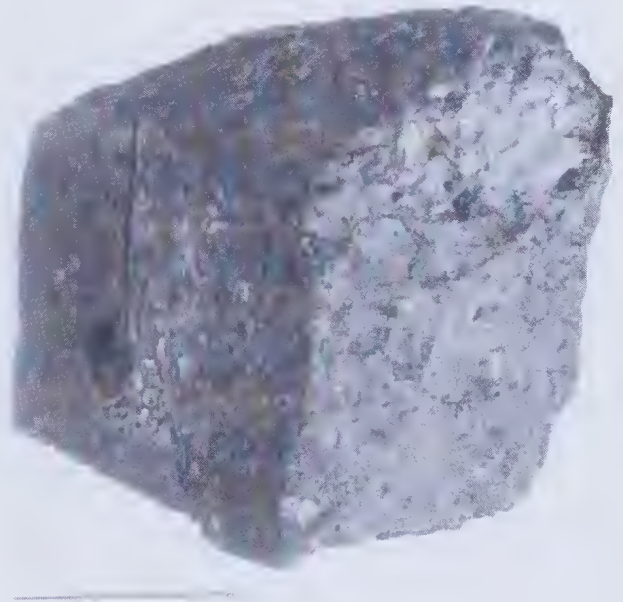


Figure 6. Mass (originally 54 kg) of the Bencubbin meteorite found in July 1930. Scale bar is 10 cm. (photograph by K Brimmell).

similar to the CR group of carbonaceous chondrites and an unique Antarctic chondrite Allan Hills 85085 (Barber & Hutchison 1991; Weisberg *et al.* 1995).

The stony-irons may have formed by the mixing of both solid and liquid metal and silicates at various depths within their parent asteroids. A close relationship between some pallasites and one of the groups of irons suggests that they may have formed in the semi-molten regions between the metallic cores and rocky outer skins of small planet-like asteroids, whereas mesosiderites originated as mixtures of solid and liquid metal and achondritic rocks of diverse origins.

Recovery of meteorites in Australia

Currently, fragments from a total of 474 distinct and authenticated meteorites have been described from Australia. The material comprises 389 stones (21 achondrites, 366 chondrites and 2 unclassified stones), 71 irons, 13 stony-irons and one meteorite of unknown class. One meteorite, Murchison Downs, previously thought to be distinct has been shown by Bevan & Griffin (1994) to be a transported fragment of the Dalgara mesosiderite and is not included in the total. Two hundred and fifty-seven distinct meteorites are currently known from Western Australia, 123 from South Australia, 48 from New South Wales, 20 from Queensland, 12 from the Northern Territory, 10 from Victoria and 4 from Tasmania. Discoveries include the first lunar meteorite, Calalong Creek, found outside of Antarctica (Hill *et al.* 1991).

Only thirteen well-documented observed meteorite falls have been recorded from Australia (Bevan 1992a). The most recently recovered fall (Fig 3) is a single stone of an ordinary chondrite weighing 488.1 grams, that fell on Binningup beach in Western Australia on 30 September, 1984 (Bevan *et al.* 1988). Several large fireballs, some associated with sonic phenomena, from which meteorites may have been deposited, have been recorded in Australia over the last few years (*e.g.* see McNaught 1993). However, no known material that can be linked to these events has been recovered. A list of the authenticated observed meteorite falls from Australia is given in Table 1. One of the most recent discoveries is a 34 kg

mass of ordinary chondrite found near Broken Hill in December 1994 (Grossman 1996)

In Australia, most chance meteorite recoveries, or *finds*, have resulted from the clearing of land for agriculture and pastoralism, and also mining and prospecting activity. The distribution of meteorite falls and finds in Australia is shown in Fig 7. The general lack of discoveries in tropical Australia (north of latitude 23° S) probably reflects a climate and physiography that are not conducive to the preservation and recognition of meteorites, respectively. As noted by Mason (1974) and Bevan (1992a), there remain surprisingly few documented discoveries from central Australia and Queensland.

To date, the largest single mass of meteorite found in Australia is an 11.5 tonne fragment of the Mundrabilla iron found in 1966 on the Nullarbor Plain in Western Australia (Wilson & Cooney 1967). Since the discovery of this mass, more than twelve additional masses of the same meteorite totalling more than 22 tonnes have been recovered from a large area of the central Nullarbor in Western Australia (*e.g.* see De Laeter 1972; De Laeter & Cleverly 1983; De Laeter & Bevan 1992 and references therein).

Five meteorites (4 irons and 1 stony-iron) are associated with meteorite impact craters (Bevan 1992a, 1996). Figure 7 shows the locations of the Dalgara, Veevers, Wolfe Creek, Boxhole and Henbury impact craters. Mount Darwin crater in Tasmania (Fig 7) is undoubtedly of impact origin but no meteorites have been collected (Fudali & Ford 1979). An additional small crater, the Snelling crater, has recently been discovered in Western Australia (E S Shoemaker, *pers. comm.*). However, no meteorites are reported to have been collected from the locality. Throughout Australia another eighteen larger structures are known to varying degrees of certainty to be the deeply eroded remains of giant meteorite or asteroidal impact craters (Shoemaker & Shoemaker 1988, 1996). No meteoritic material is known from these sites although there is, in many cases, abundant evidence of meteorite impact that may include characteristic macroscopic shatter-cones, microscopic shock-metamorphic effects in the target rocks, and noble metal geochemical anomalies.

Table 1.
Australian observed meteorite falls (in chronological order)

Name	Date of fall	class	State	co-ordinates
Tenham	(spring) 1879	L6	Qld	25° 44'S 142° 57'E
Rockhampton*	(spring) 1895	stone	Qld	23° 23'S 150° 31'E
Emmaville	1900	Eucrite	NSW	29° 28'S 151° 37'E
Mount Browne	17.7.1902	H6	NSW	29° 48'S 141° 42'E
Narellan	8.4. 1928	L6	NSW	34° 3'S 150° 41' 20"E
Moorleah	Oct. 1930	L6	Tas	40° 58.5'S 145° 36'E
Karoonda	25.11.1930	CK4	SA	35° 5'S 139° 55'E
Forest Vale	7.8.1942	H4	NSW	33° 21'S 146° 51' 30"E
Millbillillie	Oct. 1960	Eucrite	WA	26° 27'S 120° 22'E
Woolgorong	20.12.1960	L6	WA	27° 45'S 115° 50'E
Wiluna	2.9.1967	H5	WA	26° 35' 34"S 120° 19' 42"E
Murchison	28.9.1969	CM2	Vic	36° 37'S 145° 12'E
Binningup	30.9.1984	H5	WA	33° 09' 23"S 115° 40' 35"E

*specimen lost

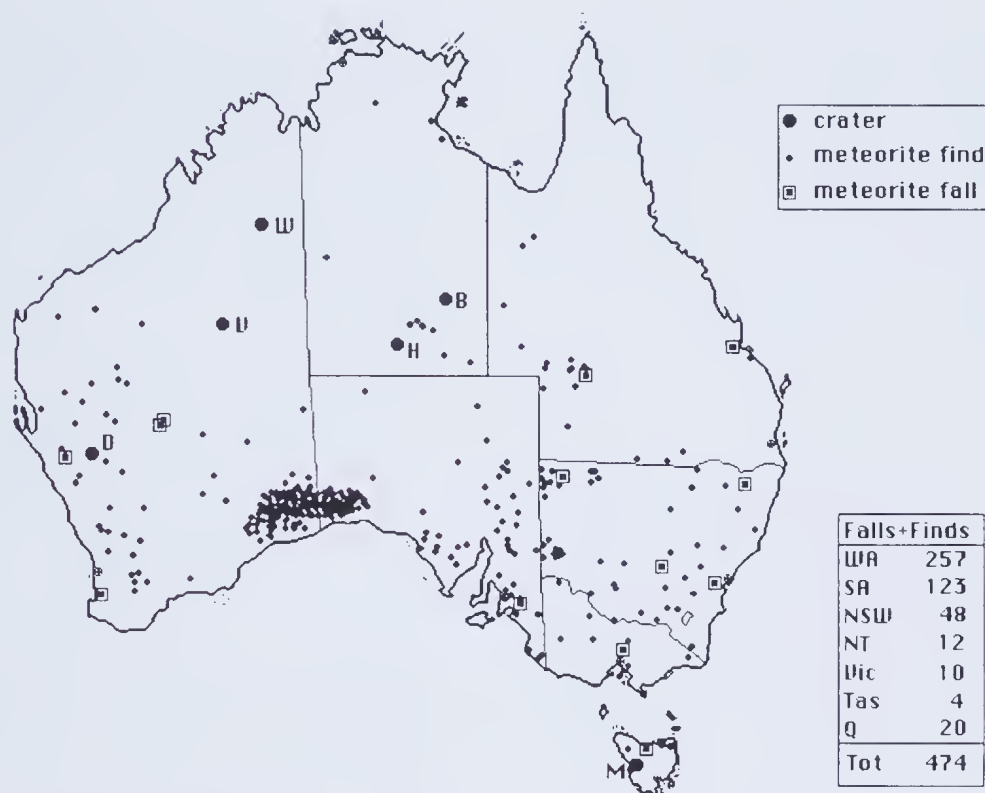


Figure 7. Geographical distribution of meteorite finds and observed falls in Australia and sites of five meteorite impact craters associated with meteorites, Wolfe Creek (W), Dalgarranga (D), Veevers (V), Henbury (H), Boxhole (B), and one crater, Mount Darwin (M), at which meteorites are lacking.

The Nullarbor Region

The anomalously large number of meteorites found in the Nullarbor Region (Fig 7) does not mean that more meteorites have fallen there than anywhere else in Australia, but reflects an unique physiographic environment and a sustained research effort to recover meteorites from the region. The Nullarbor Region is coincident with a geological structure, the Eucla Basin, that straddles the border between South Australia and Western Australia. The sedimentary basin comprises essentially flat-lying limestones of Lower-Middle Miocene Age (*ca.* 15 Ma) outcropping over an area of *ca.* 240,000 km². (Lowry 1970). The arid to semi-arid climate of the Nullarbor that has persisted for tens of thousands of years or more, combined with a lack of vegetation and pale country rock, has made the Nullarbor ideal for the prolonged preservation and easy recognition of meteorites. Essentially, meteorites have been accumulating in the Nullarbor since climatic conditions allowed for their preservation. Moreover, in the Nullarbor there is good evidence to suggest that meteorites are lying on, or near, the surfaces on which they fell and that, physiographically, the region has remained essentially undisturbed for at least the last 30,000 years (Benbow & Hayball 1992).

Many of the early meteorite recoveries from the Nullarbor resulted from a programme of search and recovery by personnel from the Kalgoorlie School of Mines (see Cleverly 1993 and references therein), although numerous recoveries have been made by rabbit trappers, notably the Carlisle family from Kalgoorlie (Bevan 1992a). Until recently, there were few meteorites

known from the area of the Nullarbor in South Australia. However, collecting by rabbiters and prospectors has resulted in a great number of new recoveries from the area that account for most of the large increase from the 50 meteorites reported by Bevan (1992a) to the current 123 known from South Australia. Unfortunately, most of this South Australian material now resides in collections outside of Australia.

Nomenclature

The described meteorites from the Nullarbor Region now account for more than 50 % of all meteorites known from Australia. As meteorites are named after the geographical localities where they are found, the general lack of geographical names in the Nullarbor, and the great number of new recoveries has caused difficulties for meteorite nomenclature. The problem has been overcome by the introduction of a system of meteorite nomenclature based on geographically named areas. Seventy-four named areas have been delineated (47 in Western Australia; 27 in South Australia) in the Nullarbor Region and new and distinct meteorites take the name of the area in which they are found and a three digit number (*e.g.* Cook 005), usually in chronological order of discovery (Bevan & Binns 1989a; Bevan & Pring 1993). Some nomenclatural anomalies have occurred and these include the Haig, Rawlinna (stone), Cook 003 and Maralinga meteorites, the localities of which lie outside the newly designated areas with the same names.

Palaeoclimatic information from meteorites in the Nullarbor Region

As soon as meteorites enter the Earth's atmosphere they are subject to contamination from, and alteration by, the terrestrial environment. Prolonged weathering transforms many of the minerals in meteorites, masks their original textures, redistributes elements, and eventually destroys them. However, the processes of weathering leave a terrestrial 'fingerprint' in meteorite finds that may be used in climatic research. Meteorites that survive prolonged weathering are potential recorders of environmental conditions during their period of terrestrial residence. Although in its infancy, the use of ancient Nullarbor meteorite finds as indicators of palaeoclimate is yielding promising results.

Recent research on meteorites from the Nullarbor and other hot desert regions of the world for which terrestrial age data are available (Jull *et al.* 1990; Jull *et al.* 1995) has suggested that the weathering characteristics of ancient meteorite finds may reflect the climatic conditions within a millennium or so of their fall (Bland *et al.* 1995a,b). This discovery has stimulated a completely new area of palaeoclimatic research, and the Nullarbor region is proving to be one of the most significant areas of the world for the use of meteorites as palaeoclimatic indicators.

Within the limits of the data currently available (Jull *et al.* 1995), the distribution of ^{14}C terrestrial ages of ordinary chondritic meteorites from the Nullarbor Region show an apparently uninterrupted exponential decrease from the present day to around 30 ka BP (Fig 8). The oldest terrestrial age of a stony meteorite yet published from the Nullarbor (27 ± 1.4 ka) is in good agreement with the estimated age (<30 ka) of the present calcareous clay cover of the Nullarbor (Benbow & Hayball, 1992).

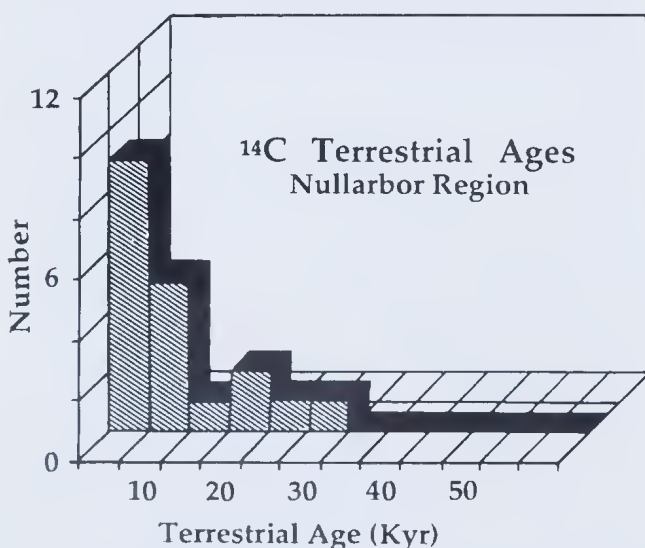


Figure 8. Distribution of ^{14}C terrestrial ages of chondritic meteorite finds from the Nullarbor Region of Australia (after Jull *et al.* 1995).

The preservation and accumulation of meteorites as the result of prolonged aridity in the Nullarbor from ca. 30 ka BP is consistent with palaeoclimatic evidence from a wide variety of geomorphological, palaeontological

and biological studies of the region. For example, a number of workers, notably Thorne (1971), have suggested on the basis of faunal remains from caves that the climate of the Nullarbor has not changed significantly during the last 20 ka (*e.g.* see Wyrwoll 1979; Davey *et al.* 1992 and references therein). However, pollen from three caves in the Nullarbor examined by Martin (1973) indicated that the period 20 ka to ca. 10-8 ka BP was slightly more arid than that of today, with annual rainfall averaging ca. 180 mm. The palynological evidence suggests that from around 10-8 ka BP to 5-4 ka BP the rainfall increased on the Nullarbor, and has since maintained an annual average of about 250 mm. Further evidence from pollen from the dessicated guts of some dated mummified mammalian carcasses (Ingram 1969), supports the conclusion that the annual rainfall in the Nullarbor Plain area has remained roughly constant since about the middle Holocene (ca. 5 ka BP).

Currently, the Nullarbor has no active surface drainage. However, higher lake levels and relict stream courses traversing the region testify to a period of greater effective precipitation (Jennings 1967a,b, 1983; Lowry 1970; Lowry & Jennings 1974; Graaff *et al.* 1977; Street-Perrott & Harrison 1984). When these channels were last active is unknown, although U-series dating of calcite speleothems from Nullarbor caves (Goede *et al.* 1990) suggests that no significant calcium carbonate deposition has taken place during the last 300-400 ka. Presently, active deposition of speleothems in Nullarbor caves is almost exclusively gypsum and halite (Goede *et al.* 1990; Goede *et al.* 1992). As a mechanism for halite deposition, Goede *et al.* (1992) suggest that periodic changes to slightly higher effective precipitation in the Nullarbor re-initiated percolation and, provided that the seepage was subject to strong evaporation in the cave atmosphere, led to the deposition of halite speleothems.

U-series ages of halite speleothems from the Nullarbor have been reported by Goede *et al.* (1990, 1992). One large (2.78 metres long) broken salt stalagmite from Webbs Cave gave a 'bulk' age indicating prolonged deposition during the Late Pleistocene between ca. 37 ka and 20 ka BP (Goede *et al.*, 1992). Previous dating (Goede *et al.*, 1990) of a small (0.16 m) halite stalagmite from the same cave yielded an age of 2.5 ± 1.2 ka indicating that there have been at least two phases of halite speleothem formation in Webbs Cave within the last 37 ka.

The work of Goede *et al.* (1990, 1992) shows that during the Late Pleistocene (ca. 30-20 ka BP) and again in the Holocene (ca. 2.5 ka BP) there were minor changes to more humid conditions in the Nullarbor following periods of prolonged aridity, and support the conclusions of Martin (1973) and Lowry & Jennings (1974). Significantly, the age range of the oldest salt stalagmite (37-20 ka) from Webbs Cave overlaps with the apparent onset of accumulation of stony meteorites from around 30 ka BP on the Nullarbor surface. If any stony meteorites significantly older than 30 ka exist in the Nullarbor, it is possible that they are buried in the calcareous clay cover. However, it should be noted that $^{26}\text{Al}/^{53}\text{Mn}$ dating of the Mundrabilla iron meteorite by Aylmer *et al.* (1988) gave a terrestrial age >1 Ma, indicating that it is the oldest meteorite fall yet recovered from the Nullarbor.

Bland *et al.* (1995a, b) have attempted to quantify the state of weathering of a number of ordinary chondrite finds from the Nullarbor using ^{57}Fe Mössbauer spectroscopy. By comparing the abundance of ferric iron oxide/oxyhydroxide species in individual meteorites against terrestrial age, Bland *et al.* (1995b) suggest that meteorite weathering is sensitive to climate at the time of fall. Moreover, meteorites appear to obtain their weathering characteristics within *ca.* 1000 years of fall. Gradual weathering rates, like those that have persisted in the Nullarbor, allow the formation of stable surface oxide layers, and a reduction in the porosity of the meteorites that provides protection against further significant weathering during periods of more effective precipitation. Moreover, carbonates derived by the meteorite from the Nullarbor limestone also fill pore space in some stones (Bevan & Binns 1989b). It appears that once a stony meteorite reaches a state of temporary equilibrium after initial weathering, the energy of the surrounding environment needs to be raised significantly to alter the remains further, or destroy them.

Figure 9 shows a plot of total ferric oxidation (%) in Nullarbor H-group ordinary chondrites against terrestrial age (after Bland *et al.* 1995b). Periods of climatic change derived from biological and geomorphological studies outlined above are marked for comparison. Even within the limits of the small data set currently available there is a remarkable co-incidence between the 'rustiness' of chondritic meteorites as measured by Mössbauer (Bland *et al.* 1995b), and periods of alternately higher and lower effective precipitation in the Nullarbor during the Late Pleistocene and Holocene.

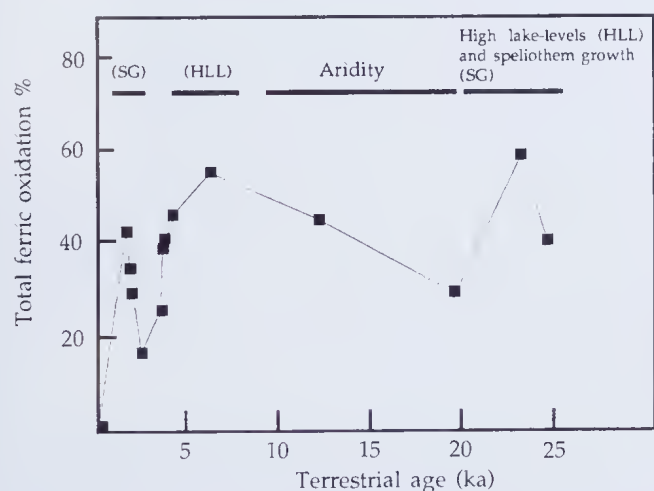


Figure 9. Plot of total ferric oxidation (%) of weathered H-group ordinary chondrites from the Nullarbor Region of Australia as determined by Mössbauer against their ^{14}C terrestrial ages. Marked above are significant palaeoclimatic events in SW Australia for the same period; see text for references (after Bland *et al.* 1995b)

Jull *et al.* (1995) have made a preliminary study of the carbonates from some weathered ordinary chondrites from the Nullarbor. The results show that there are some variations in $\delta^{13}\text{C}$, and there is a weak correlation of $\delta^{13}\text{C}$ and carbonate content with terrestrial age that may be linked to palaeoclimatic events.

Recent recoveries of rare meteorites in Australia

Bevan (1992a) listed a number of rare meteorites recovered from Australia. The most significant of the observed falls (Table 1) are the two carbonaceous chondrites Murchison [CM2] (CM= Mighei type carbonaceous chondrite) and Karoonda [CK4] (CK= Karoonda type carbonaceous chondrite; see Bevan 1992a and references therein). Carlisle Lakes, a previously anomalous and ungrouped chondritic meteorite find from the Nullarbor (Binns & Pooley 1979) has recently been shown to belong to an entirely new group of chondrites including an observed fall, Rumuruti, from Kenya (Schulze *et al.* 1994). The new group of chondrites, known as the 'R' group (after Rumuruti), includes several other meteorites from Antarctica and one from the Reg El Acfer in North Africa (Bischoff *et al.* 1994; Rubin & Kallemeyn 1989, 1993, 1994; Schulze *et al.* 1994). A new group of carbonaceous chondrites, the CR group (named after the type meteorite Renazzo), has been described (*e.g.* see Weisberg *et al.* 1993). Spettel *et al.* (1992) have suggested that Loongana 001, an unusual chondrite found in 1990 in the Western Australian Nullarbor is related to the CR group. However, Kallemeyn & Rubin (1995) have shown that the meteorite does not belong to any of the established carbonaceous chondrite groups and along with the Coolidge chondrite found in the USA, forms a distinct grouplet of carbonaceous chondrites related to the CV group (named after the type meteorite Vigarano).

Bevan (1992a) noted that out of the main groups or sub-types of meteorites then known, only ten were not represented in collections from Australia. In the last three years, however, several ordinary chondrites of petrologic type 7 have been described providing examples previously missing (Wlotzka 1994), along with a possibly new petrologic type 2 (?) member of the CV group of carbonaceous chondrites, Mundrabilla 012 (Ulff-Møller *et al.* 1993). One enstatite chondrite of type 7, Forrest 033, has been recorded (Wlotzka 1994). A new CV3 chondrite, Denman 002, has been described from the South Australian Nullarbor (Dominik & Bussy 1994).

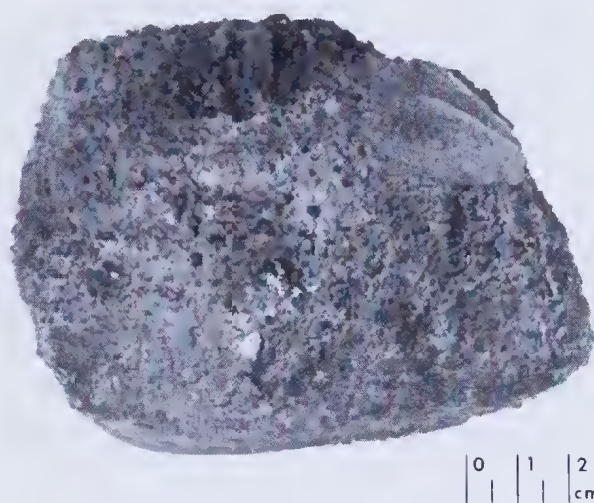


Figure 10. Mass (1 536 kg) of the Cook 003 CK4 chondrite found in the South Australian Nullarbor. The knobby surface is due to large protruding chondrules (photograph by K Brimmell).

Sleeper Camp 006 and Cook 003 (Fig 10), two stones found in the Western Australian and South Australian Nullarbor respectively, are additional CK4 chondrite finds. Cook 003 may be paired with an earlier reported discovery, Maralinga (Geiger *et al.* 1992). Two other recoveries from the Nullarbor, Camel Donga 003 and Watson 002 are the first known examples of CK3 chondrites from Australia and their reported find-sites are sufficiently far apart to discount pairing (Wlotzka 1993a,b).

In terms of achondrites, Calalong Creek (Hill *et al.* 1991; Wlotzka 1991), reportedly discovered within the strewn field of the previously known Millbillillie achondrite (eucrite) in Western Australia, is the first lunar meteorite found outside of Antarctica. Calalong Creek is a polymict lunar breccia with the highest KREEP component of any known lunar meteorite (Hill *et al.* 1991). New achondrites from the Nullarbor include several howardites; Camel Donga 004, Hughes 004, Hughes 005, Old Homestead 001, Mundrabilla 018 (Wlotzka 1995) and Muckera 002. Old Homestead 001 and Mundrabilla 018 were found close together, as were Hughes 004 and 005 and these may be fragments of the same fall. The fragments constituting Muckera 002 were found near the site of discovery of the Muckera meteorite (now Muckera 001) which is also a howardite. Eagles Nest found in central Australia and Reid 013 from the Nullarbor, two new examples of brachinaites (olivine-rich achondrites named after the type meteorite found at Brachina in South Australia) have been found (Wlotzka 1992b, 1993b). Reid 013 is remarkably similar to Nova 003, a meteorite the locality of which is uncertain (Wlotzka 1993b). Three new ureilites, Hughes 007, Hughes 009 and Nullarbor 010, have been found in the Nullarbor and the latter meteorite is similar to Nova 001, an ureilite originally reported as found in Mexico although now considered to be of uncertain location (Wlotzka 1993a).

A new lodranite (an anomalous stony-iron meteorite of rare type possibly related to the ureilite achondrites), named Gibson, has been found in north-western Australia and is the first meteorite of its kind found in Australia (Wlotzka 1992b). Since 1992, two important new masses of iron meteorites have been reported. Two distinct group IIE irons, Watson (93 kg) (Olsen *et al.* 1994) and Miles (265 kg), have been reported from the South Australian Nullarbor and Queensland, respectively (Wlotzka 1992a, 1994). A new iron, Hidden Valley weighing 7 kilograms, belonging to chemical group IIIAB was also found in Queensland in 1991 (Wlotzka 1994). These discoveries bring the total number of distinct irons reported from Australia to 71.

Meteorite groups and types remaining to be reported from Australia include chondrites belonging to EH3-4, EL5, CI, CK5, CO3, and a possibly new 'CH' group of carbonaceous chondrites (Bischoff *et al.* 1993), and achondrites belonging to the calcium-poor groups, aubrites and diogenites.

Summary

Over the last ten years, the number of meteorites known from Australia has doubled. Even so, the large number of recent recoveries probably represents a small

fraction of the meteorites that are available for collection in the country's arid and semi-arid zones. Together with meteorites from other hot and cold deserts of the world, the concentration of meteorites in the Nullarbor (Fig 11) is already providing a valuable research resource. New groups of meteorites are being recovered that are extending our knowledge of the early Solar System; statistical studies are providing information on the flux of meteorites with time; and terrestrial age dating combined with weathering studies are yielding palaeoclimatic information about the areas of meteorite accumulation.



Figure 11. Crusted fragment of the Camel Donga eucrite achondrite shower at the site of discovery on the Nullarbor Plain (lens cap for scale is 5 cm diameter).

Although various dating techniques have been applied to a wide variety of terrestrial materials (e.g. see Lamb 1977), one of the major problems of Quaternary palaeoclimatic research is the paucity of dateable materials that can provide an absolute chronology for events. Concentrations of meteorites, such as in the Nullarbor Region, provide dateable materials of a variety of terrestrial exposure times spanning the accumulation period, and may allow changes in weathering rates through time to be estimated. The pioneering work of Bland *et al.* (1995 a,b), Jull *et al.* (1995) and others is demonstrating that weathered stony meteorites have the potential to provide useful palaeoclimatic information over the period of their accumulation.

The surfaces of ancient stony meteorites from the Nullarbor frequently possess variably thick carbonate coatings (caliches) that have been derived via the calcareous clay from the limestone country rock (Bevan & Binns 1989 a,b). Additionally, extensively weathered Nullarbor stony meteorites contain veins and pockets of carbonate that have penetrated the fabric of the meteorite along cracks and pores. Detailed mineralogical and isotopic studies of carbonates from Nullarbor meteorites have yet to be performed. However, measurements of the stable isotopic compositions of these evaporitic deposits may aid in determining the source materials and the mechanisms of calichification, related to temperatures of deposition. Since these carbonates are likely to have grown much more rapidly than marine carbonates they could be used to derive high resolution temperature profiles, and offer possibilities of palaeotemperature

assessment over the time span of meteorite accumulation in the Nullarbor.

Meteorites found in Australia are playing an increasingly important role in fundamental research across a wide spectrum of disciplines both within the country and overseas. There is every reason to believe that dense accumulations of meteorites, as in the Nullarbor, exist throughout the arid zone of Australia. Eventually, Australia may outstrip Antarctica and the USA as a source of meteorite recoveries. This seemingly unlikely source of Quaternary palaeoclimatic information provides yet another aspect to meteorite research in Australia. What studies of ancient meteorite finds from Australia are likely to reveal in detail about past climates is unknown. Like all fundamental scientific research, one never knows how useful it will be until it is done!

Acknowledgements: The author thanks an anonymous reviewer for many helpful comments that improved the manuscript. Danielle Hendricks, Peter Downes, Jennifer Bevan and Kris Brimmell are thanked for their assistance in the preparation of the manuscript. John de Laeter is thanked for constant encouragement and help over many years of research into Australian meteorites.

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Isotopic anomalies in extraterrestrial grains

T R Ireland

Research School of Earth Sciences, Australian National University, Canberra ACT 0200

Abstract

Isotopic compositions are referred to as anomalous if the isotopic ratios measured cannot be related to the terrestrial (solar) composition of a given element. While small effects close to the resolution of mass spectrometric techniques can have ambiguous origins, the discovery of large isotopic anomalies in inclusions and grains from primitive meteorites suggests that material from distinct sites of stellar nucleosynthesis has been preserved. Refractory inclusions, which are predominantly composed of the refractory oxides of Al, Ca, Ti, and Mg, in chondritic meteorites commonly have excesses in the heaviest isotopes of Ca, Ti, and Cr which are inferred to have been produced in a supernova. Refractory inclusions also contain excess ^{26}Mg from short lived ^{26}Al decay. However, despite the isotopic anomalies indicating the preservation of distinct nucleosynthetic sites, refractory inclusions have been processed in the solar system and are not interstellar grains. Carbon (graphite and diamond) and silicon carbide grains from the same meteorites also have large isotopic anomalies but these phases are not stable in the oxidized solar nebula which suggests that they are presolar and formed in the circumstellar atmospheres of carbon-rich stars. Diamond has a characteristic signature enriched in the lightest and heaviest isotopes of Xe, and graphite shows a wide range in C isotopic compositions. SiC commonly has C and N isotopic signatures which are characteristic of H-burning in the C-N-O cycle in low-mass stars. Heavier elements such as Si, Ti, Xe, Ba, and Nd, carry an isotopic signature of the s-process. A minor population of SiC (known as Grains X, ca. 1 %) are distinct in having decay products of short lived isotopes ^{26}Al (now ^{26}Mg), ^{44}Ti (now ^{44}Ca), and ^{49}V (now ^{49}Ti), as well as ^{28}Si excesses which are characteristic of supernova nucleosynthesis. The preservation of these isotopic anomalies allows the examination of detailed nucleosynthetic pathways in stars.

Introduction

The study of isotopic anomalies in meteorites offers a direct image of nucleosynthesis in stars and the processes by which dust is dispersed into the interstellar medium. The solar system is composed of a mixture of a variety of nucleosynthetic sources which were homogenized during the solar nebula and further during planetary formation. Isotopic abundances on Earth are affected only by radioactive decay and by the relatively small fractionations caused by the differences in the masses of the isotopes during kinetic processes. The largest fractionations are found in H (which has the largest mass difference between two isotopes) and fractionation effects become smaller with increasing mass. However, in different nucleosynthetic environments in stars, there are large (orders of magnitude) variations in isotopic production rates. The preservation of material from these distinct environments results in grains with diverse isotopic compositions.

The measurement of isotopic compositions generally involves the measurement of a ratio of one isotope to another in a mass spectrometer. For an element with more than three isotopes, an isotopic composition is said to be anomalous if it cannot be related to the terrestrial (and by inference solar) composition through a mass fractionation law that describes the behaviour of the isotopes in physicochemical processes including the

measurement process itself. A mass fractionation correction can be achieved by using one isotopic ratio to determine the fractionation and then removing that degree of fractionation from the other isotopic ratio(s). A fractional deviation of a fractionation-corrected ratio is often reported such that a deviation of zero is normal, positive indicates the ratio exceeds normal and negative indicates it is below normal. For an element with only two isotopes, a mass fractionation correction is not possible and the isotopic ratio is said to be anomalous if it exceeds the range of that ratio typically found on Earth.

A wide variety of mass spectrometers have been used in analyzing isotopic compositions of meteoritic phases. Gas and solid-source mass spectrometers require multigrain samples to achieve sufficient signal for a precise analysis but have clearly characterized various mineralogical grain types (diamond, silicon carbide, graphite) as highly anomalous. But perhaps the most telling information is coming from ion microprobe analysis which allows the measurement of single grains (to sub-micron sizes) for a number of elements and isotopic systems which can then be related to distinct astrophysical settings.

This paper gives a brief introduction to nucleosynthesis in stars, gives an overview of some of the isotopically anomalous extraterrestrial grains found so far, and relates these to some distinct astrophysical settings which are possible sites for grain formation. It is not intended to be comprehensive review of all knowledge of the isotopic systematics of extraterrestrial grains but has been written to give a more general outline of the field along

with some illustrative examples. More detailed reviews and information can be found in Lee (1988) and Clayton *et al.* (1988) for isotopic systematics of refractory inclusions, and Anders & Zinner (1993) and Ott (1993) for interstellar grains. The role of ion microprobe mass spectrometry in these fields has been reviewed by Ireland (1995).

Nucleosynthesis

Apart from ^1H , ^2H , ^3He , ^4He and ^7Li which were formed in Big Bang nucleosynthesis, all other nuclides were produced, and are being produced, in nuclear reactions predominantly in stars, but also in circumstellar environments and the interstellar medium. In light of the abundance curve of the nuclides (Fig 1), Burbidge *et al.* (1957) specified 8 modes of nucleosynthesis that could account for its features. The two fundamental thermonuclear reactions driving stars are *H-burning* and *He-burning*. Upon exhaustion of the H, the star contracts under its own gravity and if the star has sufficient mass, He will ignite and burn to form C and O. Reactions involving the successive addition of α particles (α -process) to nuclei heavier than ^{20}Ne result in four-structure nuclei (^{24}Mg , ^{28}Si , ^{32}S , ^{36}Ar , ^{40}Ca , and possibly ^{44}Ca) at higher abundances than their neighbours. For a massive star, nucleosynthesis can proceed up to the mass region of the iron group of elements where the nuclear binding energy is at a maximum per nucleon and no further energy can be released by fusion. At this stage, nuclear statistical equilibrium (*e-process*) is achieved in the reactions and leads to a build-up of Fe-group-element abundances. The low-abundance nuclides ^6Li , ^9Be , and ^{10}B and ^{11}B are unstable in stellar interiors and require formation in low temperature environments. The formation of these elements was assigned to the *x-process* (x for unknown) which is probably largely due to spallation. Burbidge *et al.* (1957) also used the x-process to explain the abundance of D, but this is now assigned to the Big Bang.

Elements heavier than the Fe group are mainly produced in neutron-capture reactions. In the *s-process*, the addition of neutrons is slow relative to the likelihood of a β decay, whereas in the *r-process* the addition of neutrons happens on a rapid time-scale and very neutron-rich nuclei can result. The *s-process* occurs in asymptotic giant branch (AGB) stars undergoing core He burning where neutrons are released through reactions such as $^{13}\text{C}(\alpha, n)^{16}\text{O}$ or $^{22}\text{Ne}(\alpha, n)^{25}\text{Mg}$. The *r-process* requires a large neutron flux and it is likely to be related to supernovae. Low abundance nuclei on the low mass side of the valley of stability (*i.e.* neutron-poor isotopes) are referred to as *p-process* nuclides and these have probably formed by photonuclear reactions, also in supernovae.

A supernova of Type II occurs when a massive star has consumed most of its nuclear fuel. At this stage it has an Fe-rich core and is surrounded by layers still burning the remnants of its fuel. Upon near exhaustion of this fuel, the star can no longer support itself gravitationally and it implodes. The rebound shock wave ejects the outer layers while the material inside the mass cut collapses into a degenerate neutron star or pulsar. Novae and supernovae of Type I involve binary stars with a white dwarf left after the AGB phase. A nova can

occur if the white dwarf accretes more than 10^{-3} solar masses of H from its companion resulting in explosive H burning. If the accreting white dwarf eventually exceeds the Chandrasekhar limit ($1.4 M_{\text{solar}}$) then the star collapses and explodes as a Type Ia supernova.

The evolution and ultimate state of a star is governed primarily by two parameters, metallicity and mass. The metallicity of a star is the proportion of elements heavier than H and He and it affects nucleosynthesis in that heavier elements can act as seeds for more energetic reactions. The mass of the star limits the ultimate temperature and pressure in the stellar core. For a star less than

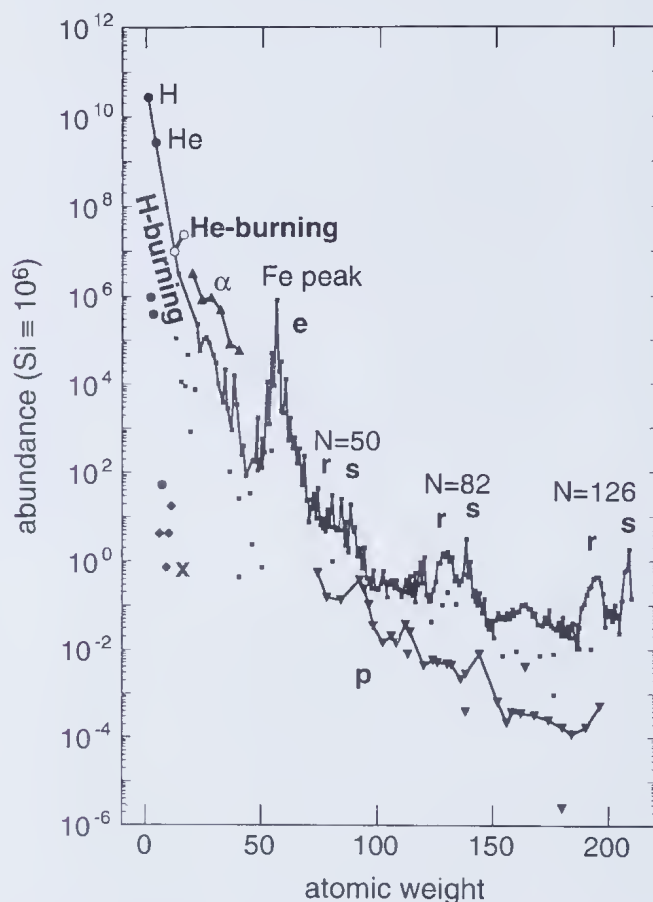


Figure 1. The solar abundances are an average of a number of different nucleosynthetic sites. Burbidge *et al.* (1957) first described the features of the nuclidic abundance curve in terms of eight discrete stellar processes and with only a little refinement the principal tenants are still applicable. *H-Burning* and *He-burning* are the fundamental thermonuclear reactions driving stars converting H to He and He to C and O. The relatively high abundances of nuclei in the mass range 20 - 40 with mass numbers divisible by 4 (*i.e.* ^{20}Ne , ^{24}Mg , ^{28}Si , ^{32}S , ^{36}Ar , ^{40}Ca) are due to progressive addition of α -particles (α -process). Stars more massive than $9 M_{\text{solar}}$ can ignite the C,O-rich core left after He burning and for the most massive stars nucleosynthesis can proceed to equilibrium burning (*e-process*) at the iron abundance peak. The *s-* and *r-processes* refer to progressive addition of neutrons at slow (*s-process*) and rapid (*r-process*) rates with respect to the competing β decays. Note the peaks in abundance of *s-* and *r-process* nuclei around magic number nuclei ($N=50, 82$, and 126). Low-abundance neutron-poor nuclei are likely due to photo-nuclear reactions (*p-process*). Finally the abundances of the light, low-abundance elements Li, Be, B as well as D, were attributed to an unknown process (*x-process*). Deuterium is now attributed to Big Bang production and the abundances of Li, Be, and B are likely from spallation of heavier nuclei.

$9 M_{\text{solar}}$, no nucleosynthesis beyond He-burning occurs and the star decays into a white dwarf. Heavier stars can ignite the C-O core and reactions proceed to build heavier nuclei (up to ^{56}Fe) with the heaviest stars eventually exploding in Type II supernovae. In the chemical evolution of the galaxy, material is ejected from a dying star to become available for the next generation. Supernovae are extremely efficient at getting a large mass of matter into the interstellar medium, but these events are uncommon since they only occur in the heaviest stars (1 event per 50 years per galaxy producing $2 M_{\text{solar}} = 0.04 M_{\text{solar}}\text{yr}^{-1}$). Most material ejected into the interstellar medium comes from the winds of AGB stars and ensuing planetary nebula (1 yr^{-1} producing $0.3 M_{\text{solar}} = 0.3 M_{\text{solar}}\text{yr}^{-1}$). Novae are more frequent but produce far less material (30 yr^{-1} producing $10^{-4} M_{\text{solar}} = 0.003 M_{\text{solar}}\text{yr}^{-1}$; Truran 1993).

Winds carry material away from the star surface into the circumstellar environment where it condenses into grains, and these grains continue to move away from the star and may be entrained into molecular clouds to form the next generation of stars. In this way, our solar system was formed in a molecular cloud that had contributions from a large number of stars of different generations.

Isotopic anomalies

Isotopic anomalies were first discovered for the noble gases Ne and Xe from chondritic meteorites (Reynolds & Turner 1964; Black & Pepin 1969). However, the systematics of the noble gases were poorly understood and an origin from within the solar system from radiogenic decay of transuranic nuclides and fission could not be dismissed. Furthermore, in the 1960s the current paradigm on the evolution of the solar nebula was that it attained sufficiently high temperatures to volatilize most if not all of the interstellar dust falling into it and therefore all isotopic heterogeneity had been removed (Cameron 1962). The discovery of isotopic variations in O, the most abundant lithophile element in the solar system quickly changed the situation (Clayton *et al.* 1973).

Refractory Inclusions

The oxygen anomalies, excesses in ^{16}O of up to 5 %, were discovered in refractory inclusions from the Allende carbonaceous chondrite. These inclusions are composed of refractory oxides that would condense from a cooling gas of solar composition, and the Allende inclusions commonly include the minerals spinel MgAl_2O_4 , melilite $\text{Ca}_2\text{Al}_2\text{SiO}_7$, $\text{Ca}_2\text{MgSi}_2\text{O}_7$, pyroxene $\text{CaMgSi}_2\text{O}_6$, and perovskite CaTiO_3 . Refractory trace elements are enriched in these inclusions at approximately 20 times that found in bulk carbonaceous chondrites indicating that the refractory inclusions could have condensed as the first 5 % of solar material. These characteristics suggested that refractory inclusions would be the best place for a search for isotopic anomalies since these early-formed solids may have crystallized before all isotopic heterogeneities were removed from the solar nebula.

With the discovery of oxygen isotopic anomalies, the race was on to find further isotopic effects. Magnesium isotopic abundances were found to give excesses and deficits in ^{26}Mg after correcting for mass-dependent fractionation (Gray & Compston 1974; Lee & Papanastassiou 1974), but large excesses of ^{26}Mg which were correlated with Al/Mg in a number of phases from a single refractory inclusion established the presence of short lived ^{26}Al in the early solar system (Lee *et al.* 1977). Excess ^{26}Mg (i.e. extinct ^{26}Al) is commonly present in refractory inclusions at a maximum level of $5 \cdot 10^{-5} \text{ }^{27}\text{Al}$.

During the final stages of hydrostatic burning in a massive star, the Fe-group elements form under quasi-equilibrium conditions since binding energy per nucleon is at a maximum. However, during the supernova the isotopic compositions of the Fe group elements could be affected by large changes in the physical conditions of nucleosynthesis. Furthermore, titanium, on the wing of the Fe abundance peak, is highly refractory and concentrated in the inclusions. Titanium isotopic anomalies were first discovered as a 0.1 %, or 1 ‰, enhancement in ^{50}Ti , a very small effect barely resolvable at that time (Heydegger *et al.* 1979). Soon, however, titanium isotopic anomalies became regarded as being ubiquitous in refractory inclusions (Niemeyer & Lugmair, 1981). Further developments in mass spectrometry revealed effects in other Fe-group elements including excesses of ^{48}Ca (Jungck *et al.* 1984), and ^{54}Cr (Birck & Allègre, 1984). The common feature of these anomalies is that they occur in the heaviest nuclides of each element and hence suggest a common nucleosynthetic component is responsible. These excesses in ^{48}Ca , ^{50}Ti , and ^{54}Cr were successfully modelled as the products of explosive nucleosynthesis around a supernova whereby reactions in the ejecta resulted in neutron-rich compositions (Hartmann *et al.* 1985). Coincidentally, a supernova had earlier been proposed not only as the source for ^{16}O and ^{26}Al but also as a trigger for the collapse of the molecular cloud into the solar system (Cameron & Truran 1977).

Refractory inclusions are also found in other meteorites besides Allende, and in particular the refractory inclusions of CM meteorites such as Murchison and Murray contain corundum Al_2O_3 and hibonite $\text{CaAl}_{12}\text{O}_{19}$. The presence of these minerals with even higher condensation temperatures than the assemblages of the Allende inclusions suggested that these might contain even larger isotopic anomalies. However, the CM inclusions were very small, seldom over 0.2 mm. The mass spectrometry of the Allende inclusions involved chemical separation of the elements of interest and then loading the separate onto a filament which was heated to a temperature sufficient to ionize the element. With such small samples from Murchison, the prospect of conventional thermal ionization mass spectrometry was not good. However, ion microprobes were beginning to be utilized in the search for isotopic anomalies and the small CM inclusions were an ideal place to start. The ion microprobe utilizes a focussed primary beam of O^+ or Cs^+ ions to sputter away the sample. Sputtering with an energetic ion beam results in a small fraction of the ejected atoms being ionized and these can be extracted and passed to a mass analyzer. The benefit of ion probe analysis is that a single inclusion can be analyzed for a

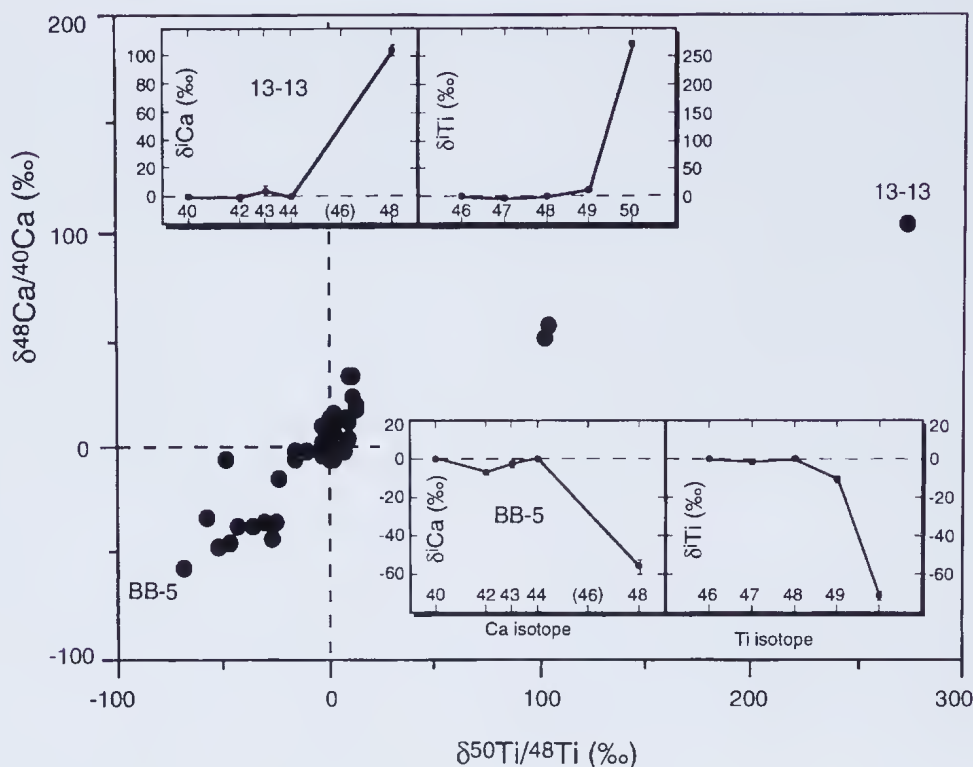


Figure 2. Ca and Ti isotopic compositions in hibonite ($\text{Ca}[\text{AlMgTi}]_{12}\text{O}_{19}$) inclusions display a large range from excesses in the most neutron rich isotopes to deficits while the other isotopes are close to solar proportions (defined as deviations, $\delta^i\text{Ca}$ or $\delta^i\text{Ti}$, in ‰). The most anomalous grains are both from the Murchison meteorite, 13-13 (Ireland 1990) and BB-5 (Hinton *et al.* 1987) which have large excesses and large depletions respectively in ^{48}Ca and ^{50}Ti (insets). The ^{48}Ca and ^{50}Ti anomalies are clearly correlated and are inferred to come from neutron-rich supernova ejecta.

variety of elements while maintaining the petrographic context.

Titanium isotopic analyses of hibonite-bearing inclusions quickly established the highly anomalous characteristics of these grains (Fahey *et al.* 1985; Ireland *et al.* 1985; Hinton *et al.* 1987) with anomalies more than an order of magnitude larger than those found in Allende. Both excesses and deficits were discovered in ^{50}Ti , and the excesses or deficits in ^{50}Ti were correlated with ^{48}Ca (Fig 2; Zinner *et al.* 1986; Ireland 1990). While the excesses in these isotopes are consistent with the addition of neutron-rich material, deficits are not so readily interpretable. Hinton *et al.* (1987) proposed that the deficits were due to the solar system being initially depleted in these neutron-rich isotopes and that the solar system received a late injection of supernova ejecta which included ^{16}O and ^{26}Al . However, oxygen isotopic analyses revealed that all hibonite inclusions were enriched in ^{16}O relative to terrestrial by 4 to 7 ‰ (Fahey *et al.* 1987; Ireland *et al.* 1992) precluding a scenario that includes a solar system initially depleted in ^{16}O . Magnesium isotopic compositions of the hibonite grains were split between inclusions that have $^{26}\text{Al}/^{27}\text{Al}$ at the canonical solar system value of 5×10^{-5} and inclusions that were below 10^{-5} .

Surprisingly, a number of morphological, chemical, and isotopic features are found to be correlated in Murchison refractory inclusions. Most of the hibonite inclusions can be divided into two types, single hibonite crystal fragments with low TiO_2 concentrations (<2.5

wt%), and hibonite-spinel inclusions with high TiO_2 concentrations (3 - 9 wt%). Most of the crystal fragments show smooth REE patterns with depletions in the more volatile REE Eu and Yb while the spinel hibonite inclusions most commonly have ultrarefractory-REE-depleted patterns. Besides the clear correlation in ^{48}Ca and ^{50}Ti anomalies, it has been noted (Clayton *et al.* 1988) that no inclusion with a large ^{50}Ti anomaly also has excess ^{26}Mg (at 5×10^{-5}), and those inclusions that have anomalies in the ultrarefractory elements of their REE patterns do have excess ^{26}Mg unless they have a Ti isotopic anomaly (Ireland 1990). These correlations and associations clearly indicate that nucleosynthetic anomalies have survived through discrete inclusion-forming events in the early solar system.

But, despite containing isotopically anomalous material, refractory inclusions are not interstellar grains. They are too large and do not preserve the effects expected of solids exposed to travel in the interstellar medium.

Presolar carbon and carbides

The progressive isolation of isotopically distinct noble gas components finally led to the isolation of presolar grains in the laboratory (Fig 3). The main processing involves the acid dissolution of solar system material with further concentration based on other physical properties such as density. It is therefore no surprise that the first interstellar grains identified are all carbon com-

pounds that are resistant to acid attack. These compounds are inferred to be of presolar origin because carbon compounds such as diamond, graphite, and SiC are unstable in the solar nebula and the grains contain material that is isotopically anomalous in the extreme.

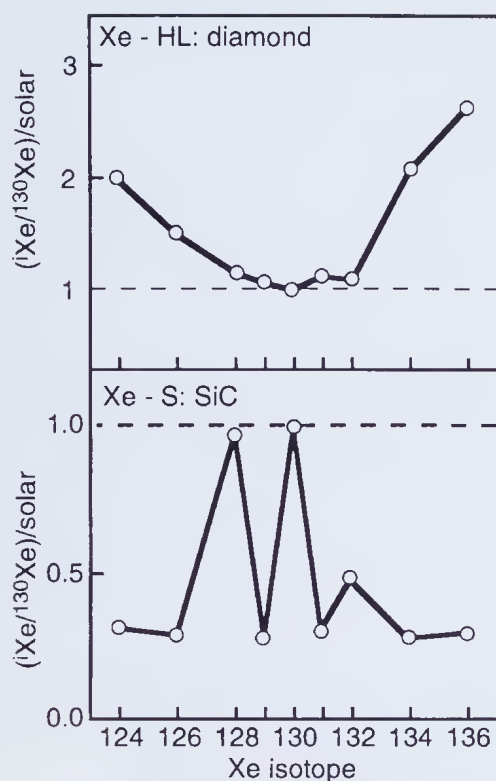


Figure 3. Progressive enrichment of these isotopically exotic Xe components led to the discovery of interstellar diamond and SiC. Interstellar graphite was discovered through isolation of a nearly pure component of ^{22}Ne . The light and heavy components of Xe-HL cannot be produced in the same nucleosynthetic event and are probably the result of mixing (Huss & Lewis 1994). The Xe-S component from SiC reflects a mixture between the composition produced in s-process nucleosynthesis and a near-normal component (Lewis *et al.* 1994).

Diamond was the first type of presolar grain recognized and has the highest abundance at 400 ppm by weight of bulk meteorite (Lewis *et al.* 1987). The diamonds have an average size of only 2 nm and a characteristic enrichment of the heavy and light isotopes of Xe (Fig 3). The small size of the diamonds means that the individual grains contain only a few hundred atoms and the chemical properties are dominated by the bonds on the surface (Bernatowicz *et al.* 1990). It remains unclear as to how the Xe atoms are located in the diamonds but the concentration levels require that there be only one Xe atom per million diamond grains. One mechanism proposed involves ion implantation of the Xe atoms, but the low concentrations of other elements neighbouring Xe in the periodic table is contrary to that expected. The exact formation environment/mechanism of the diamonds remains enigmatic. The diamonds may have been produced in shock waves from supernovae passing through molecular clouds or from chemical vapour deposition because the free energy difference between diamond and graphite is only 1kcal/mol. Support for this theory comes from the near-normal $^{13}\text{C}/^{12}\text{C}$ ratios in

the diamonds (Fig 4), although a much larger amount of graphite should have been preserved in the meteorites in these scenarios.

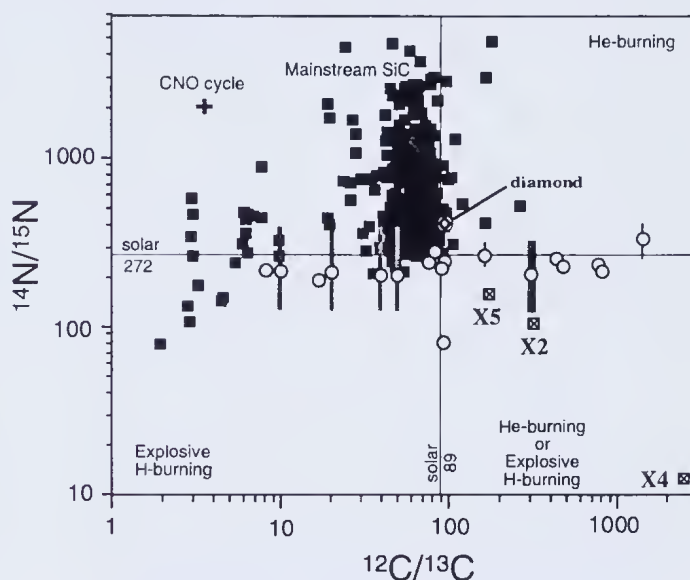


Figure 4. C and N isotopic compositions of presolar diamond, graphite, and silicon carbide. The range of C and N isotopic compositions from these grains is so large that the data is displayed on a plot of the logarithm of the ratios. Diamond has a composition close to solar (origin), while silicon carbide (squares) and graphite (open circles) show large variations. Most SiC occurs in the CNO-cycle quadrant but a suite of grains known as Grains X, which comprise ca. 1 % of SiC analyzed, have highly unusual characteristics and are plotted with a crossed square. These Grains X have other unusual isotopic characteristics as shown in Figures 5 and 6. Data from Hoppe *et al.* (1994) and Amari *et al.* (1990).

Silicon carbide was first identified from the Murray CM meteorite by Bernatowicz *et al.* (1987). It is perhaps the most fruitful of the presolar grains since it contains reasonably high concentrations of a number of trace elements and is still reasonably abundant (≈ 6 ppm). Individual grains range in size from <0.2 to around 20 μm allowing ion microprobe analysis of single grains for a variety of elements (see for example Hoppe *et al.* 1994). Ion microprobe analysis of both individual grains and bulk SiC indicated large isotopic anomalies in a number of elements, *e.g.* Si, C, N, Mg, Ti, Ba, Nd, and Sm (Bernatowicz *et al.* 1987; Ireland *et al.* 1991; Zinner *et al.* 1987, 1989, 1991a,b). The mainstream SiC grains show ^{12}C and ^{15}N enrichments (Fig 4) consistent with a mixture of CNO-cycle material with isotopically normal C and N. Most of the heavier elements analyzed from SiC qualitatively show the effects of the s-process with Si isotopic compositions enriched in ^{28}Si and ^{30}Si (Fig 5), Ti isotopic compositions enriched in the minor isotopes relative to ^{48}Ti (Fig 6), and s-process enrichments in heavier elements such as Xe (Fig 3), Ba, Nd, and Sm. These grains are likely to have formed around C-rich AGB stars and dispersed into the interstellar medium by the strong outflows from these stars. However, there are discrepancies in detail between the predicted and measured abundances. For example, the best-fit line passing through the mainstream SiC Si-isotope data has a slope of 1.3 (Fig 5) which differs from the theoretical value of ca. 0.35 for s-process nucleosynthesis.

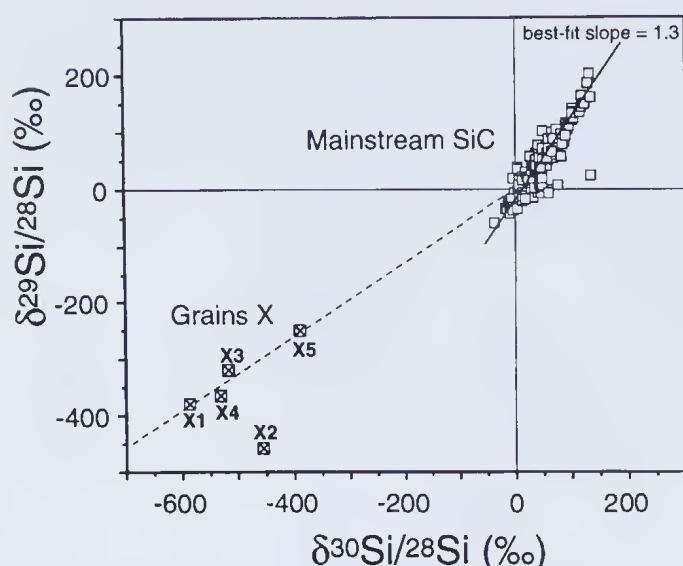


Figure 5. Si isotopic compositions of SiC grains. Most grains show elevated $^{29}\text{Si}/^{28}\text{Si}$ and $^{30}\text{Si}/^{28}\text{Si}$ ratios relative to terrestrial by up to 200 ‰. The enrichment of ^{29}Si and ^{30}Si can be ascribed to an s-process however the correlation in the $^{29}\text{Si}/^{28}\text{Si}$ and $^{30}\text{Si}/^{28}\text{Si}$ ratios indicates a slope of 1.3 which does not agree with the predicted value of 0.35 for s-process nucleosynthesis. Grains X have $^{29}\text{Si}/^{28}\text{Si}$ and $^{30}\text{Si}/^{28}\text{Si}$ ratios below terrestrial (negative delta values) and are inferred to have elevated ^{28}Si abundances which is characteristic of formation in supernova ejecta. Data from Hoppe *et al.* (1994).

A minor fraction of the SiC grains (*ca.* 1 %) show ^{13}C and ^{14}N enrichments as well as excesses of the decay products of short-lived radionuclides (Fig 6) such as ^{26}Al (now ^{26}Mg), ^{44}Ti (now ^{44}Ca), and ^{49}V (now ^{49}Ti). It appears that these short-lived nuclides are only produced together in supernovae and so Grains X may represent material from the C-rich zones in the outer layers of a presupernova star (Amari *et al.* 1992).

Graphite represents less than 2 ppm (by wt) of meteorite and of this material only a fraction is isotopically anomalous (Amari *et al.* 1990). Graphite spherules (1 to 10 μm in diameter) show a similar extreme range in C isotopic compositions as that found for SiC, but isotopically light compositions are more commonly found. Nitrogen is only present at very low levels (*c.f.* nearly 1 % in SiC) and so the lack of large anomalies in this element may not reflect the intrinsic composition. The graphite structure does not allow trace-element substitution to the same degree as SiC but the graphite spherules have been found to contain very small inclusions of refractory carbides of elements such as Si, Ti, Zr, Mo, and W (Bernatowicz *et al.* 1991). It is interesting to note that production of Zr, in particular, is characteristic of the s-process suggesting that at least a fraction of the graphite grains also come from AGB stars.

Interstellar oxides

The isolation of presolar carbon-bearing compounds was aided by their resistance to acid attack and so destruction of all the silicates and oxides in the meteorites leads to increasing concentration of these grains. However, our solar system is clearly not derived predominantly from C-rich stars but has a predominantly O-rich parentage. Most interstellar grains coming into the solar nebula must therefore be oxides but their isolation requires separation from isotopically normal solar nebula oxides which have largely the same physical properties. Nevertheless, interstellar corundum grains have been identified using similar techniques to those used in the isolation of the carbides (Hutcheon *et al.* 1994). Several grains with extreme enrichments of ^{26}Mg and ^{17}O and s-process Ti anomalies have been discovered, suggesting a source from O-rich AGB stars. However, the abundance of the corundum grains is far lower than the carbon-bearing grains suggesting that the dust in the solar nebula was predominantly in the form of silicate rather than oxide.

The stars revisited

Isotopic anomalies direct from the sites of stellar nucleosynthesis are preserved in solar system materials. Refractory inclusions preserve their isotopic anomalies despite being processed in the solar nebula, but both the chemistry and isotopic systematics of carbide grains suggest that they have presolar connections. Local chemical fluctuations allowing carbon or carbides to condense could be envisaged in the solar nebula and so their chemical instability, while supporting an exotic origin, does not preclude formation in the solar system. However, the presence of extreme isotopic anomalies in the presolar grains is the strongest indicator that they have a stellar parentage not related to our Sun. Moreover, the $^{13}\text{C}/^{12}\text{C}$

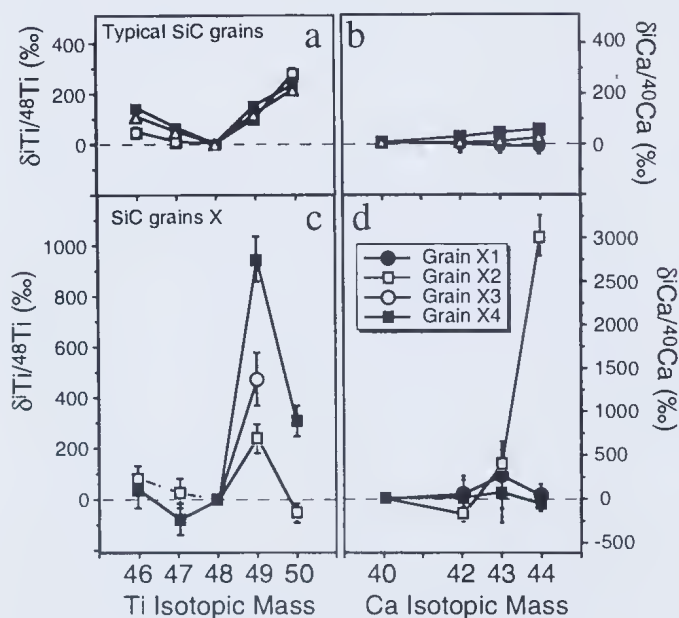


Figure 6. Ca and Ti isotopic compositions in SiC. Mainstream SiC grains have Ti isotopic compositions (a) that show enrichments in all isotopes relative to ^{48}Ti producing a characteristic V-shaped pattern. Ca isotopic compositions of mainstream SiC (b) show no large non-linear effects. Grains X on the other hand, have Ti isotopic compositions enriched in ^{49}Ti and one grain shows a large enrichment of ^{44}Ca . These anomalies are inferred to be due to the decay of ^{49}V and ^{44}Ti which are produced only in supernovae. Data from Ireland *et al.* (1991), Amari *et al.* (1992), and unpublished observations.

ratios measured from SiC and graphite show a similar range and abundance pattern to that measured in carbon stars (see Anders & Zinner 1993).

Matching isotopic characteristics with a certain class of star is not straightforward, nor in general does a unique classification become apparent. Clearly, interstellar grains must be derived from stars with strong outflow winds or that have undergone some form of explosion to distribute material into the interstellar medium. The main contributor to the SiC and graphite abundances appears to be AGB stars. Perhaps this is not surprising since these stars are common, have strong outflow winds, and hence contribute a large amount of material to the interstellar medium. A small fraction of the SiC grains appears to have been produced in a supernova. It also appears that Fe-group anomalies in refractory inclusions can be related to supernova nucleosynthesis but their isotopic characteristics appear quite different to those in the Grains X. Specifically, Ti from refractory inclusions is anomalous in ^{50}Ti (and to a lesser extent ^{49}Ti) which is related to a neutron-rich equilibrium process. On the other hand, Ti in grains X has a smooth pattern except for ^{49}Ti anomalies that are related to ^{49}V decay. Thus, Ti in the refractory inclusions appears to come from close to the mass cut of a supernova while Ti in Grains X is probably derived from the outer layers of a supernova.

A range of nucleosynthetic sites is now available for study in the laboratory and detailed nucleosynthetic calculations can now be compared with actual compositions. In large part, the agreement is quite acceptable at least qualitatively. For example, the predicted s-process compositions of the elements Xe, Ba, and Nd is in good agreement with the theoretical production. There are differences however that cannot be explained at the present time such as the slope of the Si correlation and the correlation between Si and Ti isotopes in mainstream SiC. Measurements of a wider range of elements and refinement of calculations will hopefully yield better insights into the nucleosynthetic conditions and evolution of stars responsible for the presolar dust grains.

Acknowledgments: This paper is based on a talk given at the de Laeter Symposium held in Perth November 1995 to honour the retirement of John de Laeter from the Curtin University of Technology. I am grateful to the organizers for inviting me to participate in this memorable occasion. This paper has benefitted considerably from time spent with E Zinner. M Zadnik provided a detailed review which tidied up the text.

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Solar and solar system abundances of the elements

M Ebihara

Department of Chemistry, Faculty of Science, Tokyo Metropolitan University,
1-1 Minami-Ohsawa, Hachioji, Tokyo 192-03 Japan

Abstract

With the recent progress in astrophysical observations, the solar abundances of the elements (elemental composition of the sun) can be profitably compared with the solar system abundances of the elements. In this paper, current solar and solar system abundances of the elements are reviewed and are compared; there seems to be no systematic difference. Solar system abundances of the elements are mostly deduced from the chemical composition of meteorites (mainly C1 chondrites). Compiling and evaluating the data for C2 chondrites, I once inferred that C2 chondrites also were potential candidates for the solar system standard of elemental abundances. The current data show that their abundances correlate with the solar system abundances extremely well. However better data are needed for C2 chondrites in order to ascertain if the correlation is as good as for C1 chondrites. In the near future, the solar wind will be collected by a spacecraft and yield solar abundances with quality comparable to meteorite data.

Introduction

Solar system abundances of the elements are among the most fundamental quantities in earth and planetary sciences. They are measured quantities, not physical constants, and their quality (precision and accuracy) has increased with the advances in analytical techniques. Solar system abundances of the elements are mostly based on the chemical analysis of meteorites. On the other hand, solar abundances of the elements are obtained from spectral observation of the sun. In general, the quality of the solar abundances is much poorer than the solar system abundances, although comparison of the two data sets has become possible with the great improvement in the former values in recent years.

Solar system abundances of the elements have been repeatedly presented. Among the earliest reports, the table compiled by Goldschmidt (1938) is the most famous. To estimate the solar system abundances of the elements, he used both analytical data on meteorites and observational values for the sun. From this table, Suess (1947) later deduced several rules governing the abundances of the elements in the solar system. He found that the elemental abundances were highly dependent on the stability of nuclides, and so his rules were called nuclear systematics. In 1956, Suess & Urey presented their famous table of element abundances in the solar system. They used not only data then available for meteorites and the sun, but also the nuclear systematics postulated by Suess (1947). This table was the basis of the B²FH model for the nucleosynthesis of the elements (Burbidge *et al.* 1957). During the next two decades, Cameron periodically compiled the elemental abundance data for the solar system (e.g. Cameron 1973, 1982). In those days, there were significant developments

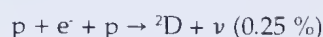
in analytical techniques (both method and instrument) for meteorites, and so not only the number was increased but also the quality of data were improved. This was a major reason why Cameron revised the abundance table at every opportunity.

In 1982, I had the opportunity of compiling solar system abundances of the elements in collaboration with E Anders (Anders & Ebihara 1982). On that occasion, we used our own analytical data for meteorites (mainly C1 chondrites) in addition to the literature data and compiled an abundance table after critical evaluation of the data. This abundance table was widely accepted by the scientific community and updated in 1989 (Anders & Grevesse 1989). There were few significant changes in solar system abundances of the elements between the two tables, because the analytical data of meteorites reported during that period were limited. In contrast, the solar abundances improved significantly. Reflecting this, Anders & Grevesse (1989) discussed solar and solar system abundances of the elements separately as well as comparatively. Their table, especially for solar system abundances is the current reference for the abundances of elements. As in the past, such compilations need to be revised, although the changes would not be great, especially for elemental abundances of the solar system. In this paper, solar and solar system abundances of the elements are reviewed and some future perspectives are presented.

Solar abundances of the elements

The outer part of the sun consists of the photosphere, chromosphere and corona; the solar photosphere is surrounded by the chromosphere and further enclosed by the corona. The energy released by the present sun is estimated to be 3.83×10^{33} erg sec⁻¹ and is believed to be supplied by nuclear fusion reactions. Judging from the current temperature and pressure estimated for the cen-

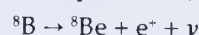
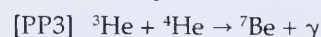
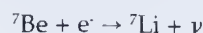
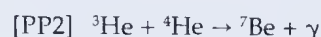
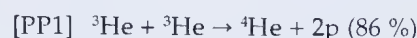
tre of the sun, it is inferred that the following reactions (named p-p chains) mainly occur inside the sun;



The deuterium produced reacts with a proton to form ${}^3\text{He}$ as follows:



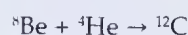
From ${}^3\text{He}$, ${}^4\text{He}$ is produced via three different paths named PP1, PP2 and PP3 as shown below;



The end result is that four protons produce ${}^4\text{He}$. Under the present conditions, the PP1 reaction is dominant whereas the PP2 and/or PP3 reactions only become significant when temperature reaches 10^7K . There is another reaction for producing ${}^4\text{He}$ from protons, called the CNO cycle, in which carbon, nitrogen and oxygen react as catalysts. This reaction becomes important only when the temperature reaches $2 \times 10^7\text{K}$. Thus there is the possibility that elemental abundances of hydrogen, helium, lithium and beryllium have changed in the sun.

How are the abundances for those elements heavier than beryllium affected in the photosphere? ${}^8\text{B}$ could be produced through the PP3 reaction shown above, but it promptly decays to ${}^8\text{Be}$ with a half-life of 0.77 sec. ${}^9\text{B}$, which is the only stable nuclide of boron ($Z=5$), could be produced by spallation reactions with heavier nuclides according to nuclear synthesis models.

In order to produce carbon ($Z=6$), the following reaction must occur:



Since the half-life of ${}^8\text{Be}$ is extremely short (10^{-16} sec), the above reaction can be initiated only at high temperatures ($> 10^8\text{K}$) and pressures (high density). Even the center of the present sun does not reach these conditions. Therefore, those elements heavier than $Z=4$ (beryllium) can be scarcely synthesized in the present sun, suggesting that (except for hydrogen, helium, lithium and beryllium) the elemental abundances of the present sun are essentially the same as those of the ancient sun 4.56 10^9 y ago.

There are several way in which the solar abundance of the elements can be determined. These are:

- photosphere (absorption intensity)
- corona (emission intensity)
- solar wind (intensity of low energy ion)
- solar flare (intensity of high energy ion)

The solar photosphere is the outermost layer of the sun, with an average depth of 400 km. It is generally believed that the photosphere has the representative elemental abundances of the sun, because the surface materials of the sun are not convected and are scarcely mixed with the inner material, which can be affected by the nuclear reactions (more extensively than the photosphere). Although the solar photosphere is thus the most suitable source for the solar abundance of the elements, there are several difficulties in obtaining reliable data. Nevertheless, precision of the solar photospheric data has steadily improved over the last two decades.

The solar abundances of the elements can be also inferred from elemental abundances of the corona, obtained either by observing emission spectra of the corona or by measuring chemical compositions of the cosmic rays it emits. Coronal emission spectra of different regions of the corona have been observed from spacecraft; for instance the corona hole, an active area, a quiet area and a prominence. Although emission spectrometry can potentially yield highly reliable data, the resulting values are not as reproducible as expected and so the solar abundances of the elements deduced from the spectra have relatively large errors (uncertainties). Cosmic rays emitted from the corona are called the solar wind and solar energetic particles (SEP). The solar wind is a current of plasma with high velocity released from the solar corona, and consists mainly of protons and electrons. Although the number of the elements measured in the solar wind is not large (<10), their abundances are in agreement with those obtained from coronal spectrometric observations. The SEP has much higher energy (up to MeV) than solar wind (measured in keV) and is emitted from the corona by several different mechanisms. The elemental abundance data for SEP are superb

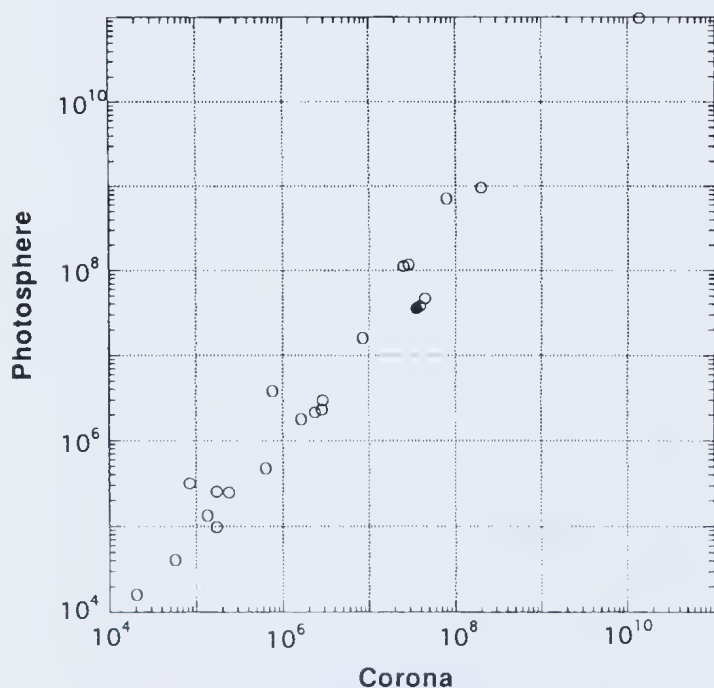


Figure 1. Coronal abundances versus solar photospheric abundances of elements. Elements of first ionization potential (FIP) $< 10\text{ eV}$ are not fractionated from Si ($\approx 3.55 \times 10^7$), which is marked by a solid circle. Elements of higher FIP are depleted in the corona by a constant factor, lying on a line parallel to that defined by the elements including Si. Data from Anders & Grevesse (1989).

in both quality and quantity compared with those for solar wind.

In Figure 1, the elemental abundances of the corona are compared with those from the photosphere. The coronal abundances are averaged values from different sources but are mostly represented by the SEP values. There seems to be a good agreement between these two sources although the coronal abundances are systematically lower than the photospheric data for several elements. These elements have a common characteristics; their first ionization potentials are consistently high ($>11\text{eV}$). This suggests that there is elemental fractionation between neutral elements (which have relatively high ionization potentials) and ionic elements (which have relatively low ionization potentials) when the elements are transferred from the chromosphere to the corona.

Solar system abundances of the elements

The solar system abundances are mostly determined from the chemical analyses of meteorites. Exceptions are hydrogen, carbon, nitrogen, oxygen and noble gas elements, which are all highly volatile. Among meteorites, C1 (or CI) chondrites have been the most extensively analyzed for this purpose. So far, nine meteorites have been recognized to be C1 or C1-like (Table 1). Of these, four were collected in Antarctica. Antarctic meteorites are susceptible to terrestrial weathering on Antarctica. In fact, Antarctic C1 (or C1-like) meteorites are not always the same as non-Antarctic C1 meteorites in chemical composition, mineralogical texture and/or oxygen isotopic composition, indicating that Antarctic C1's are not suitable specimens for measuring solar system abundances of the elements.

The terminology of "chondrite" is due to the presence of chondrules in the meteorite's texture. If this definition is strictly applied, then C1 chondrites can't be called *chondrites*, because contain no chondrules but consist of 100% matrix materials. This suggests that C1 chondrites are the richest in volatile components among meteorites. Indeed, the water content (measured as H_2O) exceeds 20% (weight %) because the matrix is composed of a large amount of hydrous silicates. Non-Antarctic C1 chondrites are all *falls* (meteorites which were observed

to fall and then collected). In contrast, Antarctic C1's are all *finds* (meteorites which were not observed to fall). Among the 4 Antarctic C1's, Y 82162 might be a real C1, but the remaining are between C1 and C2. Among non-Antarctic C1's, Revelstoke and Tonk are too small to be subjected to chemical analysis. Of the remaining three non-Antarctic C1's, Orgueil is the largest and the most frequently analyzed. Thus, solar system abundances of the elements are mostly deduced from the chemical composition of only one meteorite. There are large differences ($>10\%$) for Hf and Hg between the values of Anders & Ebihara (1982) and Anders & Grevesse (1989). For the rest of the elements, the two sets of values estimated by these authors are within 10 %.

Solar abundance values for hydrogen, nitrogen, oxygen and noble gas elements are deduced from sources other than meteorites. For these elements except noble gases, the solar photospheric data are used. For noble gas elements, each has its own method of estimation. The abundance of helium is calculated using the photospheric value of hydrogen and the He/H ratio for the HII region and/or hot stars (outside the solar system). Solar abundances of neon and argon are also derived from observations of the HII region and other extra-solar regions. However, the values estimated from measurements of prominences, the solar wind and SEP are generally in agreement with those obtained from the spectroscopy of the stars outside our solar system. For argon, an estimated (interpolated) value of ^{36}Ar based on the abundances of ^{28}Si and ^{40}Ca is also consistent with the above values. The abundances of krypton and xenon are determined from the abundances of neighboring elements. For krypton, there are two approaches; either s-process systematics or interpolations based on ^{81}Br and ^{85}Rb for ^{83}Kr , and ^{80}Se and ^{88}Sr for ^{84}Kr . The two values so obtained are similar.

Characteristics of solar and solar system abundances of the elements

Solar versus solar system abundance of the elements

The sun and other members of the solar system must have formed almost simultaneously about 4.56×10^9 y ago.

Table 1
C1 and C1-like chondrites recovered so far.

Meteorite	Year of Recovery	Place of Recovery	Fall or Find	Original Weight
<i>non-Antarctic</i>				
Alais	1806	France	Fall	6 kg
Ivuna	1938	Tanzania	Fall	705 g
Orgueil	1864	France	Fall	>10 kg
Revelstoke	1965	Canada	Fall	1 g
Tonk	1911	India	Fall	7.7 g
<i>Antarctic*</i>				
Belgica 7904	1979	Antarctica	Find	1.23 kg
Yamato 82042	1982	Antarctica	Find	37.1 g
Yamato 82162	1982	Antarctica	Find	39.5 g
Yamato 86720	1986	Antarctica	Find	859 g

*The following C1 properties (shown in parentheses) are confirmed for the Antarctic meteorites; Belgica 7904 (O-isotopes), Yamato 82042 (petrography), Yamato 82162 (O-isotopes, chemistry) and Yamato 86720 (O-isotopes).

The heterogeneity of the source material, proto-solar nebula, has been a subject of discussion for many years. There are several lines of evidence indicating that the solar nebula was heterogeneous in isotopic composition. In contrast, there are no data supporting inhomogeneity of the solar nebula in elemental abundances. The sun represents 99.7 % mass of our solar system, indicating that the elemental abundances of the sun are necessarily those of the solar system. As discussed previously, the elemental abundances of the present sun must be the same as those of the sun of 4.56×10^9 y ago for all the elements except hydrogen, helium, lithium and beryllium. Because solar system abundances of the elements are based on meteorite data, then solar abundances and solar system abundances are essentially identical for these elements except for several light elements and noble gas elements if meteorites, especially C1 chondrites, preserve the elemental abundances of the proto-solar nebula.

In Figure 2, solar and solar system abundances of the elements are compared; elemental abundances (the number of elements) are all normalized to $\text{Si} = 10^6$ atoms. As is readily apparent, elements having relative abundances of more than eight orders of magnitudes form a straight line with a slope of 0.988 ($r = 0.977$). Whenever either solar abundances or solar system abundances of the elements have been revised, such a graph has been repeatedly drawn and the extent of correlation has increased with the time. Considering that the precision of meteorite data, and especially photospheric data, has greatly improved in recent years and that the agreement between solar abundances and solar system abundances of the elements has been enhanced in recent years, it is clear that elemental abundances of meteorites, especially C1 chondrites, are essentially equal to those of our solar system.

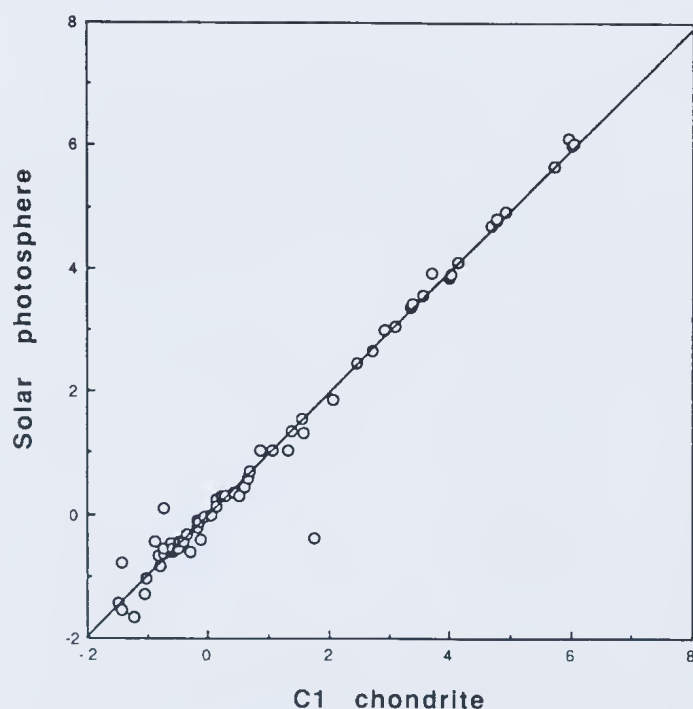


Figure 2. Solar photospheric abundances versus C1 chondrite abundances of elements; abundances are normalized to $\text{Si} = 10^6$. Only Li is located largely apart from the correlation line. From Ebihara (1992). The scale on both axes are logarithm.

Suess' nuclear systematics for solar system abundances of the elements

Suess (1947), evaluating the then available solar system abundances of the elements, found the following systematics for the abundances of the solar system nuclides:

- (a) abundances of the nuclides having an odd mass number change smoothly with increasing mass number A for the region of $A > 50$; in this case, abundances of the isobars (nuclides having the same A) are combined;
- (b) when A is even, the following variables change smoothly with increasing A ;
 - (i) for the nuclides of $A < 90$, the total abundances of the nuclides having the same I , where I is defined as $I = A - 2Z$;
 - (ii) for the nuclides of $A > 90$, the total abundances of the isobaric nuclides;
- (c) for isobaric nuclides, the nuclide having a larger I is more abundant than that having a smaller I for the region of $A < 70$; for the region of $A > 70$, the above relation is reversed;
- (d) when the numbers of nucleons (proton and neutron) correspond to so-called "magic numbers", some irregularities arise in the relationships mentioned above.

When Suess & Urey (1956) summarized the *cosmic abundances** of the elements, they used the nuclear systematics postulated by Suess (1947). They revised and even inferred several values of solar abundances based on these systematics. In later years, these revised or inferred values were replaced with the values measured in meteorites, mainly those of C1. This gave great credit to the Suess' nuclear systematics, even though it is an empirical rule. Thereafter, Suess' nuclear systematics, especially the first rule, has often been used in evaluating solar system abundances of the elements.

Abundances of odd-mass nuclides in C1 chondrites are shown in Figure 3A for $A = 59$ to 139, and Figure 3B for $A = 131$ to 209. Elemental abundances of C1 chondrites compiled by Anders & Grevesse (1989) and stable isotope abundances recommended by the International Union of Pure and Applied Chemistry (IUPAC 1991) are used to calculate relative abundances of nuclides having odd A . There appear to be some peaks in Figure 3A. The peaks at $A = 89$ and $A = 117$ to 119 correspond to the irregularity due to "magic numbers"; N (neutron number) = 50 for the former and $Z = 50$ (Sn) for the latter. A peak appearing around 130 can be explained by a relatively high probability of nuclide formation produced by p-process nucleosynthesis. In both Figures 3A and 3B, we see very smooth changes in abundances. In 1982, Anders & Ebihara (1982) identified irregularities at the

*In those days, the term "cosmic abundances of the nuclides" was often used in place of the term "solar system abundances of the elements", possibly with a tacit understanding that there was no significant difference between the two abundances. Strictly speaking, cosmic abundances of the elements cannot be obtained by analysis of any material. However, as our solar system is not special in the astronomical sense, we can assume that the solar system abundances of the elements are representative of the cosmic abundances of the elements, to a first order approximation.

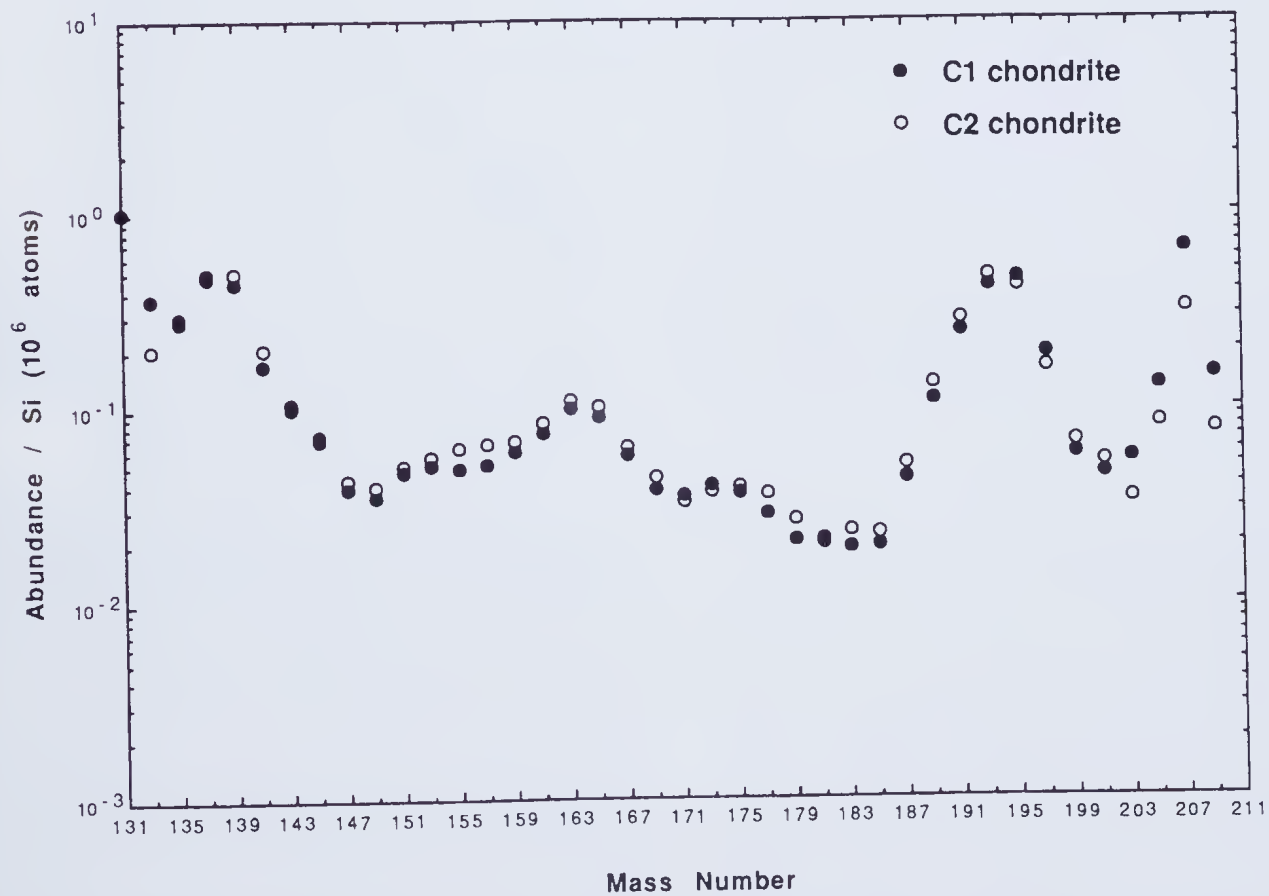
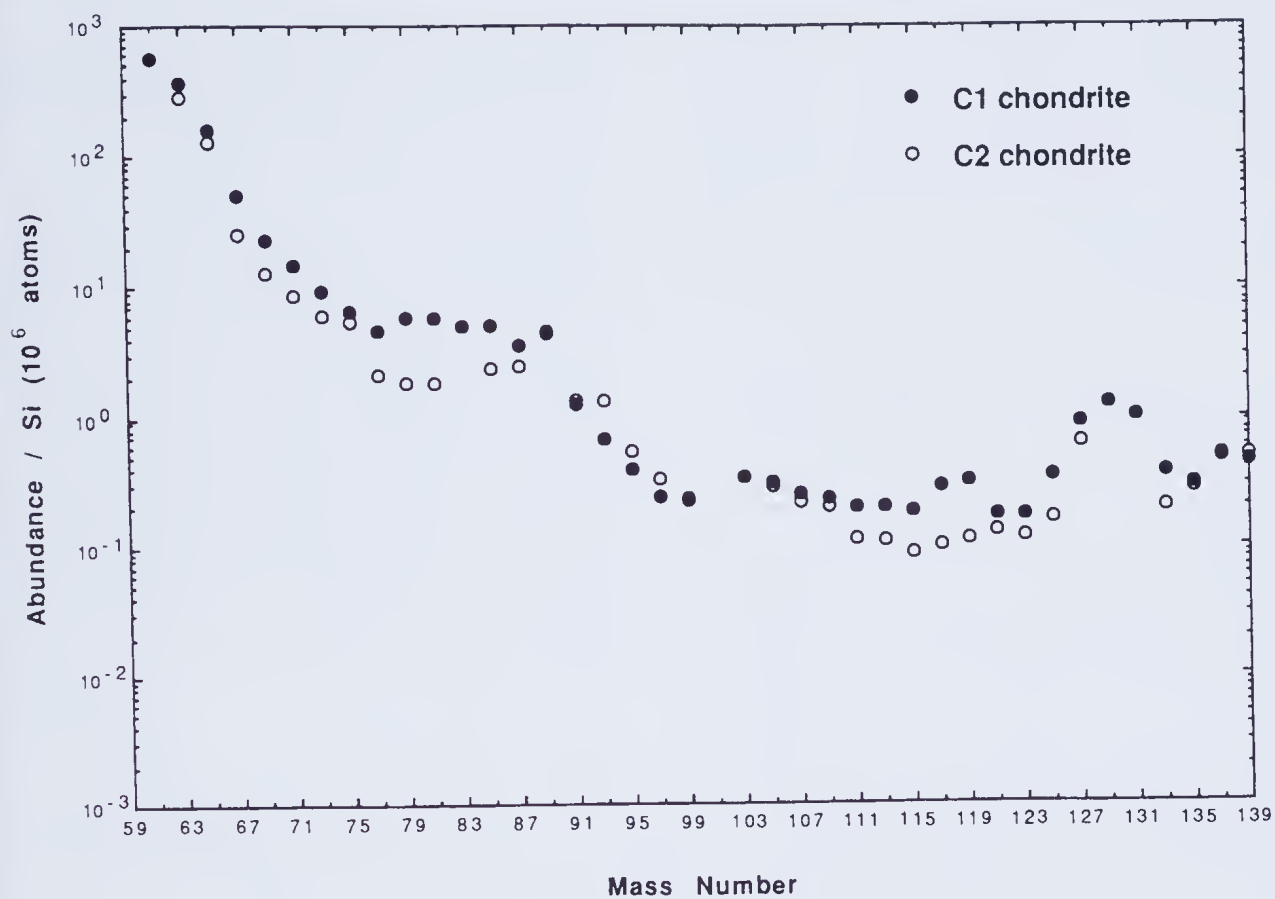


Figure 3A,B. Abundances of odd-mass nuclides from Co to La (A) and from Xe to Bi (B) in C1 and C2 chondrites. From Ebihara (1992).

Ag-Cd region and the Nd-Sm-Eu-Gd region. The former irregularity almost disappears in Figure 3A, where new and more accurate values of Ag for C1 chondrites obtained by using mass spectrometric isotope dilution technique (Loss *et al.* 1984) are used. In contrast, the irregularity at the light lanthanoid region remains unresolved. Anders & Grevesse (1989) concluded that this irregularity suggested the limitation of the Suess' nuclear systematics in evaluating solar system abundances of the elements.

Future perspective for the study on solar and solar system abundances of the elements

Do C1 chondrites yield the solar system abundances of the elements?

C1 chondrites are believed to be the most primitive meteorites and to have experienced no thermal activity since their formation at 4.56×10^9 y ago. This is supported by the observation that C1 chondrites are the richest in volatile compounds (including organic materials) and elements. However, mineralogical observations clearly show that C1 chondrite parent bodies have experienced a significant degree of aqueous alteration. (Tomeoka & Busek 1988). Chemical analyses of C1 chondrites reveal a positive correlation between the abundances of several pairs of elements (Ebihara *et al.* 1982). This correlation was interpreted to reflect aqueous alteration of the C1 chondrite parent body. Furthermore, it was recently discovered that refractory siderophile elements (Re, Os and Ir) were fractionated among ordinary and carbonaceous chondrites including C1 chondrites (Ebihara & Ozaki 1995); Si-normalized values for these elements in ordinary and carbonaceous chondrites are summarized in Table 2. It can be seen that the Os and Ir values of H chondrites are similar to those of the C1 chondrites estimated by Anders & Ebihara (1982). The Os and Ir values of C2 and C3 chondrites are nearly equal, being 5-6 % higher than those of H and C1 chondrites. For the abundance of Re, H chondrites give the highest value whereas C1 chondrites yield the lowest value. Thus, it is apparent that Re is fractionated from Os and Ir among ordinary and carbonaceous chondrites. These elements are cosmochemically grouped as the most refractory elements, and so their fractionation on the parent body

seems to be very unlikely. As Re is the most refractory of the siderophile elements, condensation and/or accretion processes must be responsible for this fractionation. Thus, it appears that C1 chondrites are not as primitive and pristine as they were once thought to be.

C2 (or CM) chondrites are much closer to C1 chondrites than any other group of meteorites (Ebihara 1992). C2 chondrites have apparently experienced aqueous alteration, to a lesser degree than C1. Elemental abundances of C2 chondrites are compared with the solar photospheric data in Figure 4. There is a high correlation between two abundances (albeit less than in Figure 2). The Suess plot for C2 chondrites is shown in Figures 3A and 3B, and is compared with that for C1 chondrites. C2 chondrite abundances change as smoothly as those of C1. The quality of the data for C1 chondrites are much better than that for C2 chondrites, because C1 chondrites have been analyzed much more extensively than C2 chondrites, and there has been greater scrutiny of data.

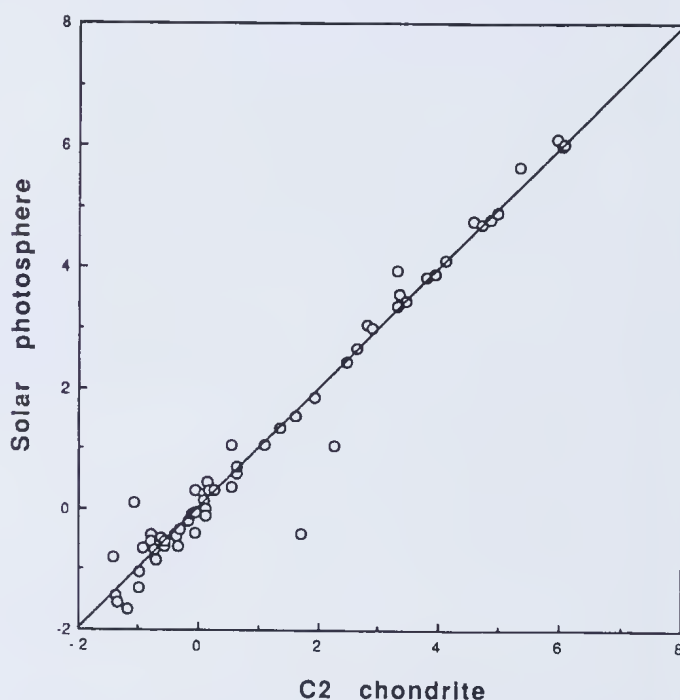


Figure 4. Solar photospheric abundances versus C2 chondrite abundances of elements; abundances are normalized to $\text{Si}=10^6$. From Ebihara (1992). The scale on both axes are logarithm.

Table 2

Atomic abundances of Re, Os and Ir in carbonaceous and ordinary chondrites (relative to 10^6 Si atoms)^a.

Meteorite groups	Re	Os	Ir
<i>Carbonaceous</i>			
C1			
A&E ^b	0.0507	0.717	0.660
A&G ^c	0.0517	0.675	0.661
C2	0.0589	0.740	0.685
C3	0.0619	0.769	0.715
<i>Ordinary</i>			
H	0.0665	0.723	0.669
L	0.0353	0.403	0.366
LL	0.0258	0.324	0.270

^aEbihara & Ozaki (1995); ^bAnders & Ebihara (1982); ^cAnders & Grevesse (1989).

From the comparison of C1 and C2 abundances on Figures 2,3 and 4, it can be concluded that C2 chondrites may also be an alternative choice as a solar system standard. The number of C2 falls is several times the number of C1 falls. Unfortunately, the quality of analytical data for C2 chondrites doesn't seem to be as high as that for C1. The essential question is, which meteorites are the most suitable for evaluating the solar system abundances of the elements? Can C1 chondrites still claim the status as the solar system standard? Or, can C2 chondrites be substituted for C1 chondrites? The propriety for being the solar system standard should be judged by the consistency with solar abundances of the elements rather than the abundance of volatile materials/elements. It is regrettable that the quality of data for solar abundances is much poorer than that for meteorites even at present, and it is unlikely that the situation will

change in the near future. Data sources for solar abundances of the elements which can be analyzed with quality comparable with that for meteorites are required.

Solar wind as a promising source of the solar system abundance of the elements

Solar wind is a source of data for solar abundances of the elements which is independent of the solar photosphere. Only a few elements (hydrogen, helium, carbon, nitrogen, oxygen, neon, silicon, argon and iron) have so far been determined in the solar wind. He/H ratios are relatively easily determined by observation from spacecraft. It is well known that the He/H ratio of solar wind varies over minutes to days by a factor of more than 100. With a systematic variation between solar minimum and solar maximum, the mean value for half a year becomes constant, 0.053 to 0.050; this is considerably smaller than the value adopted for the solar system (~0.1). Solar wind abundances of noble gas elements having small *Z* (helium, neon and argon) were determined by the Apollo mission (Geiss *et al.* 1972) which exposed to solar wind aluminum and platinum foils spread on the surface of the moon for several hours to days. These foils were then returned to earth and analyzed by noble gas mass spectrometry. The results showed that the particle flux changed in the short term, but that the relative abundances of elements and isotopes were essentially constant. Elemental abundances of helium, neon and argon deduced from observation of the HII region are in agreement with those obtained from solar wind and SEP. For carbon, nitrogen, oxygen, silicon and iron, the data obtained by the ISEE-3 satellite are available; the data for oxygen and iron are fairly reliable while those for the remaining elements cannot be regarded as representative of the solar wind.

It seems to be impossible to improve the quality of the data for solar wind using the present techniques and methods. To overcome this, a long-term collection of solar wind and/or a high sensitivity analytical method for chemical and isotopic measurements is needed. For the first alternative, a proposal is the collection of solar wind by spacecraft, similar to the Apollo moon foil experiments. For such measurements a spacecraft is required to stay in space as long as possible, and finally return to the earth. It is highly probable that this will be realized early in the 21st century.

Acknowledgments: The author thanks the symposium committee for the opportunity to present this paper on the occasion of the de Laeter Symposium on Isotope Science. This work was supported in part by Grant-in-Aids for Scientific Research of the Ministry of Education, Science and Culture, Japan (No. 0545012).

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Origin of the terrestrial planets and the moon

S R Taylor

Department of Nuclear Physics, Research School of Physical Sciences
Australian National University, Canberra, ACT 2000

Abstract

Our ideas about the origin and evolution of the solar system have advanced significantly as a result of the past 25 years of space exploration. Metal-sulfide-silicate partitioning seems to have been present in the early dust components of the solar nebula, prior to chondrule formation. The inner solar nebula was depleted in volatile elements by early solar activity. The early formation of the gas giant, Jupiter, affected the subsequent development of inner solar system and is responsible for the existence of the asteroid belt, and the small size of Mars. The Earth and the other terrestrial planets accreted in a gas-free environment, mostly from volatile-depleted planetesimals which were already differentiated into metallic cores and silicate mantles. The origin of the Moon by a single massive impact with a body larger than Mars explains the angular momentum, orbital characteristics and unique nature of the Earth-Moon system. The density and chemical differences between the Earth and Moon are accounted for by deriving the Moon from the mantle of the impactor.

The relation of the terrestrial planets to the solar system

The early history of the rocky terrestrial planets has to be placed in the broader perspective of the evolution of the solar system. They constitute such a tiny proportion of the original solar nebula that to a first approximation they could be ignored, except that we are standing on one of them. A basic question is whether the Earth and the other planets were formed by breakup of the gaseous solar nebula, or assembled "brick by brick" from smaller bodies. Were they formed in the nebula while the main gaseous and icy constituents were present, or had the hydrogen, helium, water, methane and ammonia, that constituted 99.5% of the primordial nebula, been dispersed before the formation of the inner planets? Why is Jupiter so large and what effect has it had on the rest of the system? Why is Mars so tiny, compared not only with the Earth, but to massive Jupiter? Why is there such a small amount of matter in the asteroid belt? Why is the Earth, and apparently Venus and Mars, depleted in volatile elements? Is this a local or more widespread phenomenon? Did the Earth accrete from a local zone in the nebula, or was there widespread mixing and homogenization in the early nebula? What is the relationship of the Moon to the Earth and what effect did the Moon-forming event have on the early Earth?

The solar nebula

The solar nebula initially separated as a small, slowly rotating, fragment of a molecular cloud. This allowed the formation of a single star surrounded by a rotating disk instead of the more common formation of a double star system, that constitute about 80% of all stars. Probably the disk was non-axisymmetric, which would allow both the inward flow of mass and the outward transfer of

angular momentum (*e.g.* Boss 1988). Astrophysical evidence suggests lifetimes of a few million years before the nebula is dispersed. The composition of CI carbonaceous chondrites is very close to that of the solar photosphere for non-gaseous elements, and so is probably the best estimate available for the composition of the earliest condensed material from the solar nebula. Recent work has resolved the previous outstanding anomaly of distinctly different iron abundances: the new solar values now match the CI iron abundances (Holweger *et al.* 1990).

Once the Sun has acquired about one third of its present mass, temperature and pressure conditions in the interior allowed H burning to begin. Observations on young stars suggest that the Sun underwent violent T Tauri and FU Orionis outbursts as it proceeded on its evolutionary path toward the main sequence. Strong stellar winds began to disperse the nebula, thus limiting the ultimate size of the Sun (*e.g.* Shu *et al.* 1987). Early violent solar activity may sweep away not only the H, He and other gaseous elements, but also ices and volatile elements not condensed or trapped in planetesimals large enough (metre-km size?) to remain in the inner nebula.

Loss of volatile Rb relative to refractory Sr and of volatile Pb relative to refractory U and Th appears to be widespread in the inner portions of the early nebula. Venus, Earth and Mars all appear to be depleted in volatile elements, as shown by their low K/U ratios, and by the U/Pb and Rb/Sr isotopic systematics in the case of the Earth. This depletion appears to be typical of the entire inner solar system out to perhaps 3 AU, at which distance more primitive asteroids begin to dominate the asteroid belt (Bell *et al.* 1989; Gaffey 1990). The age and initial Sr isotopic data from meteorites (Tilton 1988) record a single massive loss of volatile Rb relative to refractory Sr effectively at T_0 , so that this was a nebular-wide event rather than being connected with isotopic evolution in individual parent bodies. The depletion of

volatile elements must have occurred through physical processes (e.g. sweeping out of fine material by early solar winds) at relatively low temperatures, so that the nebula was cool at that stage.

Chondrules

Among the earliest events in the solar system was the formation of chondrules. These mm-size quenched silicate droplets form one component of chondritic meteorites. The other main constituent is the fine-grained matrix, complementary in composition to the chondrules, being notably enriched in Fe. Thus, the chondrules are not simply remelted matrix, and some segregation of the iron-rich matrix from the iron-poor chondrule precursor material must have occurred prior to the chondrule-forming events.

Formation of chondrules occurred in the nebula, rather than in any type of planetesimal or asteroidal environment (Taylor *et al.* 1983). They formed by a fast flash-melting type of process that did not change the composition of the parent material significantly (Lofgren & Russell, 1986; Radomsky & Hewins, 1988; Hewins 1992). It is not possible to cool molten drops so rapidly in a hot nebula, so the process must have been highly localised in an overall cool environment (Wood 1987). Various scenarios exist to explain these observations of which the nebular flare model appears to be most consistent with observations (Levy & Araki, 1989). What was the nature of the chondrule precursor material? Metal, sulfide and silicate phases existed already in the early nebula, either as interstellar dust grains, or condensed from nebular gas (Grossman *et al.* 1988). How was the silicate dust melted preferentially, without involving the metal and sulfide phases to more than a minor extent? Perhaps silicate dust was separated from metal and sulfide, either by differential gravitational settling or magnetically in the case of the metal, or perhaps the silicates stuck together more efficiently (Scott *et al.* 1988).

The planetesimal hypothesis

A fundamental question about the origin of the Earth concerns the state of the precursor material prior to planet formation, and the mode of accretion of the planets. Did the terrestrial planets form directly from the dispersed dust and gas of the nebula or were they built up brick by brick from planetesimals? The concept that the Earth accreted cold from fine-grained dust and gas was long postulated by Urey (e.g. Urey 1952). The striking chemical heterogeneity of the planets and asteroids (Wasson 1985; Taylor 1988) argues against simple condensation models.

Several observations suggest that the inner planets are the end products of a hierarchical accretionary process that first produced a large number of planetesimals which were later accreted to form the larger planets (Safronov 1969; Wetherill 1986). What sort of evidence do we have for these now vanished objects? A major piece of evidence comes from the tilt or inclination of the planets to their axis of rotation. The largest impact is required to account for Uranus. Calculations show that a body the size of the Earth, crashing into that planet would be needed to tip it through 90° (Benz & Cameron 1989). Smaller collisions are needed to account for the tilt of the other planets, but a few very large objects must

have been responsible, since the impacts of many small bodies will average out (Benz *et al.* 1989).

The variable rotation rates of the planets may also be a consequence of giant impacts late in their accretional history. Venus, in contrast to the Earth, has a low obliquity, and is rotating slowly backwards. These properties may result from the accretion of Venus from many small bodies, and from the lack of a giant impact on that planet (Wood 1986; Wood, pers. comm.). It is also usually considered that the absence of a primitive terrestrial atmosphere is due to its early collisional removal. In this interpretation, Venus has retained a massive atmosphere due to the lack of large atmosphere-removing collisions with that planet. The high metal/silicate ratio of Mercury is best explained by stripping of much of the silicate mantle during a large collisional event, other hypotheses encountering many difficulties (Benz *et al.* 1988). Finally, the long-standing problem of the origin of the Moon is resolved by the impact of an already differentiated massive (0.14 earth mass) body with the Earth, the material making up the Moon being mostly (>80%) derived from the silicate mantle of the impactor (Benz *et al.* 1989).

How many objects were there and how big were they? Prior to the final sweep-up into the four terrestrial planets, Wetherill (1986) calculates that 100 objects of lunar mass, ten with masses exceeding that of Mercury, and several exceeding the mass of Mars should form. He further estimates that perhaps one-third of these objects, which would provide a total of 50-75% of present Earth mass, struck the Earth.

The formation of Jupiter

Early formation of Jupiter (318 Earth-masses) appears to be required for several reasons. The planet forms early enough to deplete the asteroid belt (which now contains only 5% of lunar mass) in material, and to be responsible for the small mass of Mars (0.11 Earth-mass). This low density region of the nebula seems unlikely to have been a primary feature of the nebular disk even if the disk was non-axisymmetric. Jupiter must also form before the gaseous components of the nebula were dispersed. Other models such as the giant gaseous protoplanet hypothesis call for the formation of the planets by fragmentation of the primordial solar nebula. Jupiter should be the prime example of such a process. However, there are two principal objections. The moment of inertia data for Jupiter show that it possesses a central core of 15-20 earth masses. At the prevailing conditions in the center of Jupiter (40 mbars, 20000 K) rock and ice will be miscible with the gaseous components (Stevenson 1985). It will thus not be possible for a core to "rain-out" in the manner of a terrestrial planetary metallic core, where there are both significant density differences and metal-silicate immiscibility at the temperatures and pressures within the Earth (3.5 mbars, 5000 K; Stevenson 1985). Thus it is necessary to form a massive core first, which can then collect the gas by gravitational attraction.

A second objection is that Jupiter does not possess the solar bulk composition that would be expected if Jupiter were derived from a fragment of the primordial nebula; this gas giant has a (rock+ice)/(H+He) ratio about 10 times that of the Sun. Both these properties are readily explicable in terms of the planetesimal hypothesis.

However, it is first necessary to form a central core of 15-20 Earth masses, which can then collect the H and He envelope by gravitational attraction. How did such a large nucleus form so rapidly and so early at 5 AU from the Sun? A plausible scenario has been suggested by Lissauer (1987). As early strong solar winds associated with the T Tauri stage of stellar evolution sweep out the uncondensed components from the inner nebula, water ice will condense at about 5 AU at which location the nebular temperature falls below about 160 K. This condensation causes a local increase in particle density of the nebula at such a "snow line", which will also act as a "cold trap" for other components. Rapid accretion of a large ice and rock core can thus occur at this unique location, and act as a nucleus to collect a hydrogen and helium envelope. The low gas/(ice + rock) ratio in Jupiter implies that by the time that the core of Jupiter had grown large enough to collect a gaseous envelope, the gaseous nebula was already being dispersed, and that Jupiter simply ran out of material.

Accretion of the inner planets in a gas-free environment

Once Jupiter has formed, this massive planet dominates subsequent evolution of the solar system. After a few million years, the gas is gone and the ices and other volatiles have been swept away, so that the inner planets accreted from the left-over rocky debris. Depletion of material in the asteroid belt occurs both from accretion of material to Jupiter, and subsequent pumping up of eccentricities and inclinations of the asteroids remaining, so that the survivors have been unable to collect themselves into a planet. Others are tossed out of the system entirely. The asteroid belt appears to have existed from the earliest times. Thus the belt was not a very good quarry from which to obtain material for the inner planets. The accretion of Mars took place in a zone depleted in planetesimals from the same cause (early formation of Jupiter) and this region, at 1.5 AU again does not seem capable of supplying much material for Venus or the Earth.

Differentiation of precursor planetesimals

What was the history of the planetesimals prior to their incorporation into the inner planets? Some of the largest, the size of Mars, would have made respectable planets in their own right if fate had taken a different course. Were they already differentiated into silicate mantles and metallic cores before they came to a violent end as they were swept up into Earth or Venus?

Based on evidence from meteorites, even some relatively small planetesimals underwent internal differentiation into metallic cores and silicate mantles within a few million years of T_0 (4570 my). The larger planetesimals had already gone through a melting episode, with silicate mantle and metallic core formation, before they were accreted by the inner planets (Gaffey 1990; Taylor & Norman 1990). Such bodies of course may have been broken up by collisions and reaccreted in differing proportions of metal and silicate fractions, so that much diversity of composition among the accreting bodies can be expected.

This question of heat supply for early planetesimal melting and metamorphism is essentially unresolved. Two principal mechanisms are currently discussed. If

^{26}Al ($t_{1/2} = 730\,000$ years) was present in the early solar system (Podosek & Swindle 1988), it could have constituted an important heat source. The second possibility is by inductive heating during the early intense T Tauri and FU Orionis stages of solar activity. Both of these mechanisms encounter difficulty and early planetesimal heating may be the result of processes not presently understood (J A Wood, pers. comm.).

A crucial question for the terrestrial planets is the width of the feeding zones from which they accumulated (Wetherill 1985). The limited data for Venus show similar K/U ratios to the Earth of about 10^3 . This, coupled with the similar uncompressed density (about 4.0 g cm^{-3}) for the two planets, their similar size and their small separation of about 0.3 AU suggests that they accreted from a similar suite of planetesimals. Mars is less dense (uncompressed density 3.75 g cm^{-3}) and has a high obliquity and fast rotation rate, indicative of collisions with large objects. It is more volatile-rich than either Earth or Venus, having a K/U ratio of about 1.5×10^3 . Thus Mars, about equidistant from the Earth and the main asteroid belt, appears to be distinct from both, suggesting that there was very little mixing within the nebula over distances greater than about 0.5 AU. The survival of zoning in the asteroidal belt also points toward rather limited mixing. Other evidence includes the rarity of xenoliths of one class of meteorite in another. The great diversity in oxygen isotopic compositions (Thiemens 1988) including that of the chondrules (Grossman *et al.* 1988) is also strongly indicative of very limited mixing. In addition, the various classes of chondrites do not show simple chemical interrelationships which might indicate a heliocentric variation in composition. The general failure to identify specific classes of meteorites as building blocks for the terrestrial planets (e.g. Taylor, 1988) suggests that the inner planets accreted from rather narrow zones in the nebula, without incorporating much material from the location of the present asteroid belt.

The terrestrial Mg/Si ratio

The upper mantle of the Earth is depleted in Si and has an enhanced Mg/Si ratio relative to that of the primitive solar nebula. The bulk Mg/Si ratio of the Earth is uncertain since we do not know the Mg/Si ratio of the lower mantle. The debate over this question is unresolved (e.g. Anderson 1989). Recent suggestions that mantle plumes, responsible for hot-spot volcanism, are derived from the core-mantle boundary (Griffiths & Campbell 1991; Sleep 1992), imply that the whole mantle is involved and that there is significant mixing between upper and lower mantle. If the lower mantle of the Earth has the same Mg/Si ratio as the upper mantle, then the implications for the accretion of the Earth are considerable. In this event, the Earth accreted from a set of planetesimals with non-CI Mg/Si ratios. The variation in Mg/Si in chondrites covers such a wide range that the existence of planetesimals with higher Mg/Si ratios seems possible. This would imply a very large reservoir of planetesimals at about one AU with Mg/Si ratios significantly higher than solar.

Core-mantle relationships

The highly siderophile elements would have been efficiently extracted into the metal core under equilibrium

conditions. However the present upper mantle was apparently never in equilibrium with the core, for the abundances of Re, Au, Ni, Co and the platinum group elements (PGE= Ru, Rh, Pd, Os, Ir, Pt), although low, are higher than predicted (Arculus & Delano 1981; Delano 1986; Newsom & Palme 1984; Newsom 1986). Late accretion of CI planetesimals rich in PGE is a common explanation for their over-abundance in the upper mantle. The addition of the metallic core of the impactor responsible, in the single impact hypothesis, for the origin of the Moon (Benz *et al.* 1989) is another possible source of material. A cometary influx might be an equally viable source, although the high impact velocities of comets derived from the outer solar system may cause removal rather than addition of material.

The 'predestination' scenario (Taylor 1983; Taylor & Norman 1985; Murthy & Karato in press) in which the terrestrial planets accrete from planetesimals which were already mostly differentiated into metallic, silicate and sulfide phases implies little further reaction between metal and silicate once these bodies accreted to the Earth. In this scenario the core mantle relationships were mostly established at low, and not high pressures.

A further consequence may be noted. The metallic core of the Earth contains about 10% of a light element. The two current contenders are oxygen and sulfur. Although meteorites are not a perfect analogue for the terrestrial precursor planetesimals, they do tell us that elemental and mineralogical fractionation was endemic in the early nebula. If silicate, sulfide and metal phases, formed under low-pressure equilibrium conditions, were already present in the accreting planetesimals, separation of these phases may occur concomitantly with accretion and thus there may be little high-pressure equilibration between core and mantle in the Earth. Thus it seems unlikely that oxygen entered the core, since this requires megabar pressures. Sulfur then becomes the most viable candidate for the light element in the earth's core. Since metal-sulfide-silicate equilibria was accomplished predominantly at low pressures in precursor planetesimals, troilite will be the main source of sulfur.

Late Veneers

A number of possible effects of late additions to the Earth have been proposed. Thus comets are often invoked as a source of water (e.g. Chyba 1987). A cometary source may also account for the difference in the atmospheric abundances of the rare gases in the Earth, Venus and Mars (Owen *et al.* 1992). This concept is attractive since, in the scenario developed here, the inner solar system is depleted in water and other volatiles. Furthermore, the terrestrial water budget, although uncertain, probably constitutes less than 500 ppm of the mass of the Earth (Bell & Rossman 1992; Thompson 1992). This is less than $1/_{1000}$ of the water budget in the primitive nebula and could readily be supplied by a few large comets. Such stochastic processes also rather conveniently account for the differences among the terrestrial planets: the vexed question of the missing water on Venus is simplified if that planet never had any to begin with. Comets, however, may be a fickle source of atmospheres and hydrospheres, since they impact with relatively high velocities and thus may remove as much material as they contribute (e.g. Melosh & Vickery 1989).

There are various other unresolved problems with the concept of late veneers. The Moon shows no evidence of such events and the Moon remains "bone-dry".

Mercury

A large impact is probably responsible for the strange fact that Mercury has such a small rocky mantle and such a large iron core, and an inclined orbit so close to the sun. Two explanations are current. The first proposes that the silicate was boiled away in some early high temperature event, connected with early solar activity (the surface temperature on the present sunlit side of Mercury is 425 °C, and hot enough to melt lead). However, extremely high temperatures of several thousand degrees are required to boil off the rocky mantle. The alternative explanation, is that Mercury was struck by a body about $1/_{6}$ of its mass at a late stage in its accretion. The collision fragmented the planet with most of the silicate lost to space but the iron core surviving to reaccrete with a depleted silicate mantle (Benz *et al.* 1988). If Mercury has a plagioclase-rich crust analogous to the lunar highlands, then it is likely to be depleted in the more volatile elements, since flotation of such a crust in a magma ocean requires a water content less than 0.1% (Walker & Hays 1977). Attempts to secure a K/U ratio for Mercury, which would shed some light on these interesting problems, should be accorded a high priority.

The origin of the Moon

The broad aspects of lunar evolution are well understood. The moon was partially or wholly melted at, or shortly after, accretion. This vast mass of molten silicate has been termed the "magma ocean" and a high temperature and rapid mode of origin for the moon is required to account for it. The crystallisation of the magma ocean is understood in principle (e.g. Taylor 1982; Warren 1985). Feldspar was an early phase to crystallise. It floated, due to the low density of the feldspar crystals and the anhydrous nature of the silicate melt, and formed a thick feldspathic crust by 4440 my. Convection during cooling may have swept "rockbergs" of feldspar together, accounting for the variations in crustal thickness. A small lunar iron core about 2-5% by volume formed in the centre. This sequestered the siderophile elements. The lunar mantle was fully crystallised by about 4400 my, and resulted in a zoned silicate mineralogy, from which the mare basalts were derived much later by partial melting. This cumulate hypothesis for the source region of mare basalts is well established (e.g. Taylor & Jakes 1974; Fujimaki & Tatsumoto 1984). As the silicate minerals crystallised, those trace elements which were excluded from their crystal lattices were concentrated in the residual melt. The final stage of magma ocean evolution was the intrusion of this residual liquid into the feldspathic highland crust. The fluid was enriched in elements such as Th, U, Zr, Hf, Nb, K, REE, P (from which the acronym KREEP has been coined) and is responsible for the extraordinary near surface abundance of elements such as K, U, Th, and REE, which may be concentrated by factors of several hundred relative to bulk moon or primitive nebula values. It pervaded the crust, with which it was intimately mixed by the continuing meteoritic bombardment. The final event in crustal evolution was the intrusion of an Mg and KREEP-rich suite of rocks, produced perhaps by sub-crustal melting

induced by the impacts of giant planetesimals. Bulk moon models which contain more than 5% Al_2O_3 provide the best match to the seismic velocity profile, implying that the moon is enriched in refractory elements relative both to the Earth and to primitive solar nebula levels. This conclusion has been confirmed by data from the Clementine mission (Lucey *et al.* 1995)

Hypotheses of lunar origin

The major models for the origin of the Moon can be grouped into five separate categories, which include;

- (a) capture from an independent orbit;
- (b) fission from a rapidly rotating Earth;
- (c) formation as a double planet;
- (d) disintegration of incoming planetesimals; and
- (e) Earth impact by a Mars-sized planetesimal.

All fail to account for the unique nature of the Earth-moon system except the last. This process accounts for the high angular momentum ($3.45 \times 10^{41} \text{ rad g cm}^2 \text{ sec}^{-1}$) of the Earth-Moon system and the non-equatorial lunar orbit as well as providing extreme temperature conditions which can produce an initially molten Moon and the bone-dry features of lunar geochemistry. Computer simulations of the giant impact hypothesis under conditions that form a lunar mass depleted in metallic iron in terrestrial orbit clearly indicate that it is mostly the material from the silicate mantle of the impactor that finishes up in the Moon (e.g. Cameron & Benz 1991). This conclusion is reinforced by the geochemical problem of the failure to match Earth mantle and lunar compositions for a number of crucial elements (e.g. Taylor 1986a,b; Newsom & Taylor 1989).

The similarity in oxygen isotopes between the Earth and Moon indicate derivation of both the Earth and the impactor from the same region of the nebula, thus excluding models that derive the impactor from the outer reaches of the solar system. The similarity in $^{53}\text{Cr}/^{52}\text{Cr}$ ratios (^{53}Cr is derived in part from short-lived ^{53}Mn) between the Earth and the Moon and their contrast with higher meteoritic values (Lugmair & Maclsaac 1995) carries the same implication of derivation of lunar material from around 1 AU. A third constraint is the relatively low collision velocity (Benz *et al.* 1989; Cameron & Benz 1991) required to produce a Moon-sized body, which again restricts the impactor to be a nearby object. If the material in the Moon is derived from the impactor, then that body had a lower Rb/Cs ratio than the Earth. The primitive lunar initial $^{87}\text{Sr}/^{86}\text{Sr}$ ratios indicate that the impactor must have been depleted in Rb relative to Sr very close to T_0 .

Current models assume that core-mantle separation occurred in both the impactor and the Earth before impact, to account for the lunar siderophile element abundances and the lunar depletion in iron (13% FeO) relative to primordial solar nebula volatile-free abundance levels (as shown by the CI meteorites) of 36%. The abundance of FeO in the mantle of the impactor must however have been greater than that of the terrestrial mantle (8% FeO), since the bulk Moon contains a much higher abundance. Mars, in contrast, has a mantle FeO content of 18%.

Effects on the Earth of the Moon-forming impact

The important consequence of the single giant impact event for the Earth was that the energies involved are sufficient to melt the Earth. However, such melting is probably inevitable if the Earth was accreted from a hierarchical suite of planetesimals, regardless of whether the Moon-forming event occurred. Any primitive atmosphere is removed, which probably accounts for the very much lower ^{36}Ar content (by about two orders of magnitude) of the terrestrial atmosphere compared with that of Venus.

The lack of geochemical evidence for early differentiation of the Earth (e.g. McFarlane & Drake 1990) analogous to that shown by small-scale terrestrial layered intrusions (e.g. Skaergaard, Stillwater) or by the Moon may be due to the scale of the event. Thus a molten terrestrial mantle may be turbulent, and crystals may not have had the opportunity to settle, thus precluding large-scale fractionation (Tonks & Melosh, 1990)

In addition to the accretion of the impactor's core, about 10% of the mass of the Earth's mantle is added from the impactor's mantle. The models of Benz *et al.* (1989) indicate that most of the metal core ends up in the Earth, with the metal penetrating the mantle and ending up wrapped about the Earth's core. Such an event would not disturb siderophile abundance patterns already present in the Earth's mantle. However, a significant amount of material from the impactor's core, enriched in siderophile elements, will probably be vaporized and redistributed into the mantle.

Conclusions

1. Depletion of volatile elements in the inner nebula occurred effectively at T_0 before the chondrules were formed and affected the solar nebula out to about 3 AU. The probable mechanism was dispersal of uncondensed volatiles by early strong stellar winds during the T Tauri stage of solar evolution.
2. Jupiter formed early before the gas component in the nebula was totally depleted.
3. Accretion of the Earth, inner planets and the asteroid belt took place in a gas-free environment in the inner solar system following the formation of Jupiter.
4. The terrestrial planets were built from precursor planetesimals that had survived the clearing of the inner solar nebula. The larger ones had already formed metallic cores and silicate mantles and had already experienced at least one episode of melting and differentiation.
5. Because this metal-sulfide-silicate fractionation occurred largely at low pressures, the geochemistry of the core and mantle may instead be dominated by the low-pressure equilibria established in the precursor planetesimals. Sulfur becomes a viable candidate for the light element in the core.
6. Only limited mixing occurred in the inner nebula during planetary formation, with accretionary zones perhaps 0.3 AU wide. Very little material from the asteroid belt was incorporated in the Earth.
7. The Moon formed as the result of a single giant impact of a Mars-sized body with the Earth. Most of the

material in the Moon came from the mantle of the impactor.

8. The Earth was melted either as a result of the Moon-forming event, or as a consequence of its accretion from a hierarchical sequence of planetesimals.

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Cosmogenic noble gases in silicate inclusions of iron meteorites: Effects of bulk composition on elemental production rates.

O Jentsch & L Schultz

Max-Planck-Institut für Chemie, 55020 Mainz Germany

Abstract

The influence of bulk chemical composition on elemental production rates of neon has been studied experimentally by investigating mineral samples separated from the iron meteorites Four Corners, Landes, Linwood and Zagora. The neon in these samples is purely cosmogenic and its isotopic composition indicates an enhanced production of ^{21}Ne . This is due to the production of additional secondary neutrons caused by a larger multiplicity in meteorites of high-Z bulk chemistry.

Introduction

Meteoroids as meter-sized bodies are irradiated in space by high-energy cosmic-ray particles that penetrate these bodies and interact with its matter. Bauer (1947) and Huntley (1948) independently proposed that measurable amounts of He should be produced in iron meteorites. Paneth *et al.* (1952) showed that this was indeed true and that cosmic-ray produced $^3\text{He}/^4\text{He}$ ratio is in the range 0.2 to 0.3 and were thus very different from atmospheric He. Soon thereafter, also cosmogenic Ne and Ar isotopes were discovered (Reasbeck & Mayne 1955; Gentner & Zähringer 1957). Since then, cosmic-ray produced ("cosmogenic") stable or radioactive reaction products have been studied in great detail to investigate the irradiation history of extraterrestrial matter or the nature of cosmic rays in the past (see *e.g.* Anders 1962; Lal 1972; Reedy *et al.* 1983; Vogt *et al.* 1990).

The production rate of cosmogenic nuclides is dependent on the chemical composition of the target material, the properties of the incident particle irradiation, and the shielding conditions (pre-atmospheric size of the meteoroid and sample's location within the meteoroid). The effects of shielding are mainly caused by the fact that in nuclear reactions initiated by primary cosmic rays secondary particles are also produced. These secondary particles, mostly neutrons of smaller energy, cause further nuclear reactions. Elemental or isotopic nuclide ratios produced by these low-energy particles are different from those of the primary high-energy irradiation. Thus, the shielding of a sample is characterized by elemental or isotopic ratios of specific cosmogenic nuclides produced in different percentages by primary and secondary particles. For example, for shielding corrections of production rates of stony meteorites, cosmogenic $^{22}\text{Ne}/^{21}\text{Ne}$ is commonly used (*e.g.* Eugster 1988), or for iron meteorites, the $^4\text{He}/^{38}\text{Ar}$ ratio (*e.g.* Voshage & Feldmann 1978) is a measure for shielding.

The production rates of cosmogenic nuclides depend twofold on the bulk chemical composition of the meteor-

ite. First, the production of a particular nuclide is given by the concentration-weighted sum of the individual elemental production rates from each target element in the meteorite and, secondly, the elemental production rates themselves depend on it since spectra and intensities of secondary particles inside the meteoroid are influenced by the mean mass number and the mean atomic number of the bulk meteorite. In particular, the multiplicity for the production of secondary neutrons is greater in metal-rich meteorites compared to stony meteorites.

The latter ("matrix") effect was first suggested by Begemann & Schultz (1988). This idea is based on measurements of cosmogenic noble gases in metal and silicates of mesosiderites (Begemann *et al.* 1976). These authors had observed that the concentration of cosmogenic ^{38}Ar produced from Ca in silicates (mainly by secondary neutrons) is larger than expected from the ^{38}Ar produced in metal by the primary irradiation. Begemann and Schultz (1988) show that the production rate ratio of ^{38}Ar from Ca to that of ^{38}Ar from Fe is correlated with the total bulk metal content of mesosiderites. Also, the $^{22}\text{Ne}/^{21}\text{Ne}$ ratio in these silicate samples is relatively low. This is explained by an enhanced production of ^{21}Ne via secondary neutrons and the reaction $^{24}\text{Mg}(n,\alpha)^{21}\text{Ne}$.

The matrix effect was also treated theoretically by Michel *et al.* (1990) and Masarik & Reedy (1994) using model calculations which combine spectra of primary and secondary particles derived from Monte Carlo calculations of intra- and internuclear cascades with thin-target cross sections of the underlying nuclear reactions. These calculations show, for example, that the matrix effect is most pronounced in the production rate of ^{21}Ne from Mg, and compared to stony meteorites the ^{21}Ne production is enhanced by a factor of up to two in silicate inclusions of iron meteorites.

We report here measurements of concentration and isotopic composition of neon in silicates separated from three IA iron meteorites with silicate inclusions (Landes, Linwood and Zagora) and from the IB iron Four Corners. This work was carried out to obtain information on the matrix effect in iron meteorites which are more metal-rich than the previously investigated mesosiderites.

Experimental Methods and Results

Carbon and silicate phases of Landes and Zagora were separated from the meteorite by anodic dissolution of the FeNi. After several ultrasonic treatments and quenching steps with liquid N₂, a further separation of different grain size fractions took place using density and magnetic separation techniques. The Four Corners and Linwood separates were obtained from R S Clarke (Washington DC) and are leftovers from investigations by G P Merrill and E P Henderson.

The concentration of the elements Mg, Al, Si, K, Ca, Ti and Fe of selected separates was determined using x-ray fluorescence (XRF) techniques. The isotopic composition and concentrations of noble gases were measured using apparatus and experimental procedures as described by Schultz *et al.* (1991). Results are given in Table 1 together with estimates of the mineral composition of the samples calculated from its chemical composition.

Figure 1 shows isotopic ratios of neon in a 3-isotope plot. Cosmogenic ²⁰Ne/²²Ne ratios in ordinary chondrites are rather independent of shielding (²⁰Ne/²²Ne = 0.84 ± 0.02) and are found in a narrow area (Fig 1; hatched, marked "Chondrites"). If the measured neon is a mixture of cosmogenic gas and a trapped component (solar or

planetary gas, atmospheric contamination) the data points would be shifted to higher ²⁰Ne/²²Ne values. The low ²⁰Ne/²²Ne values indicate, however, that no significant abundance of trapped Ne is present in spite of trapped Ar, Kr and Xe that is commonly observed in silicate inclusions of iron meteorites (Hintenberger *et al.* 1969; Niemeyer 1979; Crabb 1983; Jentsch & Schultz 1987). The displacement of many data points to higher ²¹Ne/²²Ne values is discussed below.

The three feldspar-rich samples are characterized by smaller ²⁰Ne/²²Ne and ²¹Ne/²²Ne ratios. This is due to the relatively high concentration of Na in these samples. Sodium is an element that has a high production rate for ²²Ne compared to that of the other two neon isotopes. Smith & Huneke (1975) observed ²⁰Ne/²²Ne ratios < 0.7 in plagioclase separated from ordinary chondrites. Our feldspar measurement of Zagora is very similar to this value. The two Landes samples with a smaller percentage of feldspar (and thus Na) are located on the mixing line between the "pure" feldspar neon ratio and "normal" cosmogenic neon. Unfortunately, the concentration of Na was not measured directly in these samples because NaNO₃ was used to make the tablets for XRF-measurements.

Table 1.

Chemical and mineralogical information on the investigated separates as well as on their concentration and isotopic composition of neon.

Meteorite and sample #	Mg	Al	Si	K	Ca	Ti	Fe	Mg/(Mg+Al+Si)	Mineral composition				²⁰ Ne	²¹ Ne	²² Ne	²² Ne/ ²¹ Ne
	[wt %]							[wt.% ratio]					[in 10 ⁻⁸ cm ³ STP/g]			
									Opx	Ol	Cpx	Fsp				
[wt.%]																
Four Corners																
401	19.5	1.22	26.5	0.075	2.50	0.13	3.8	0.414	67	12	12	9	348.1	407.9	394.6	0.967
Landes																
I364	22.4	0.11	26.0	0.022	1.20	0.12	4.0	0.462	81	14	5	-	78.5	89.4	91.3	1.021
I344	21.9	0.35	25.7	0.021	1.59	0.13	4.3	0.456	79	14	7	-	75.2	85.5	88.0	1.029
I363	26.9	0.09	23.0	0.016	.78	0.07	3.8	0.539	42	54	4	-	84.8	97.7	98.5	1.008
I355	4.6	9.90	31.2	0.36	1.95	0.07	2.9	0.100	22	-	-	78	15.2	17.1	19.9	1.161
II345	22.2	0.37	25.6	0.027	1.42	0.13	4.3	0.460	78	15	7	-	79.7	91.2	92.8	1.017
II365	23.1	0.23	25.3	0.022	1.14	0.17	4.1	0.474	74	21	5	-	60.5	68.9	70.3	1.021
II366	26.0	0.11	23.7	0.015	0.69	0.08	3.7	0.522	53	44	3	-	89.9	103.2	103.8	1.006
II353	5.4	9.40	31.2	0.33	1.98	0.07	2.6	0.117	26	-	-	74	20.2	22.7	26.4	1.162
III343	21.4	0.44	25.1	0.021	2.38	0.13	5.0	0.456	70	17	13	-	75.3	85.8	87.6	1.021
III347	25.2	0.21	23.7	0.010	1.49	0.10	3.9	0.513	49	43	8	-	86.5	99.8	100.9	1.011
Linwood																
425	11.5	3.49	30.8	0.21	3.23	0.14	2.7	0.252	43	-	13	44	32.3	36.6	36.1	0.987
Zagora																
I329	23.0	0.22	25.4	0.015	1.12	0.13	4.1	0.473	76	19	5	-	91.6	108.2	104.3	0.964
I417	24.4	0.15	24.6	0.015	0.99	0.12	3.9	0.496	65	31	4	-	118.0	139.1	133.5	0.960
I328	22.2	0.24	25.5	0.023	1.21	0.14	4.8	0.464	63	32	5	-	113.7	133.7	129.2	0.966
II322	23.5	0.07	24.3	0.013	0.81	0.11	5.9	0.490	70	27	3	-	110.8	130.2	125.4	0.963
II320	24.3	0.09	24.1	0.017	0.86	0.11	5.1	0.501	64	33	3	-	110.1	129.9	124.0	0.955
II319	23.7	-	23.3	0.026	1.05	0.10	7.1	0.504	59	36	5	-	112.6	132.6	127.5	0.962
II325	25.3	0.08	22.8	0.020	2.54	0.09	4.3	0.525	33	52	15	-	119.6	141.9	135.1	0.952
III386	0.94	11.8	32.8	0.63	1.82	0.05	2.1	0.021	9	-	-	91	20.8	23.1	35.2	1.523

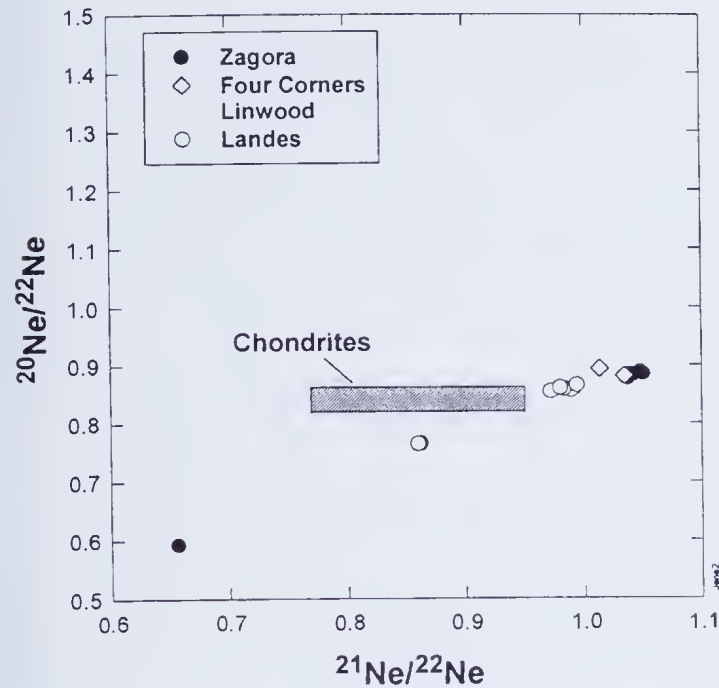


Figure 1. A three-isotope plot of neon showing the position of cosmogenic neon in chondrites (hatched area) and those of analyzed minerals separated from iron meteorites. Trapped components or atmospheric contamination, characterized by high $^{20}\text{Ne}/^{22}\text{Ne}$ and low $^{21}\text{Ne}/^{22}\text{Ne}$ values, are not present in appreciable amounts. Data points below the chondritic values are feldspar-rich samples with higher concentrations of sodium that cause higher production rates of ^{22}Ne .

Discussion

An enhanced flux of secondary neutrons in FeNi-rich meteorites will produce lower cosmogenic $^{22}\text{Ne}/^{21}\text{Ne}$ due to the reaction $^{24}\text{Mg}(n,\alpha)^{21}\text{Ne}$. To show this effect one must refer to a similar Mg concentration between normal chondritic samples and silicate inclusions of iron meteorites. In addition, the minimum values of cosmogenic $^{22}\text{Ne}/^{21}\text{Ne}$ for chondrites must be known.

For stony meteorites the shielding effect has been studied on individual samples as well as on samples taken from drill cores of meteorites. Eberhardt *et al.* (1966) found a relation between cosmogenic $^3\text{He}/^{21}\text{Ne}$ and $^{22}\text{Ne}/^{21}\text{Ne}$ that is widely used for shielding correction of production rates. This relation - originally observed in samples of different chondrites - is shown in Figure 2 together with a number of measurements for samples taken from defined locations in larger meteorites or, as in the case of Kokubunji, taken from different samples of a meteorite shower. A lower limit of observed cosmogenic $^{22}\text{Ne}/^{21}\text{Ne}$ ratios is about 1.06. This value was also confirmed in measurements of the largest stony meteorite analyzed so far, the Jilin chondrite (Begemann *et al.* 1995). These data are shown in Figure 3. Jilin has had a two-stage exposure history, a short 4π irradiation as a meteoroid and an extended one in 2π geometry (Begemann *et al.* 1985). All data have $^{22}\text{Ne}/^{21}\text{Ne} > 1.06$ but the measured concentrations of ^{21}Ne vary by a factor of about 6. They do not follow the expected variation of the production rate with shielding (e.g. Eugster 1988) as indicated by the heavy curve in Figure 3. The Jilin data clearly show that the lower limit for $^{22}\text{Ne}/^{21}\text{Ne}$ in chondrites is about 1.06. The calculation of exposure ages

using $^{22}\text{Ne}/^{21}\text{Ne}$ as a shielding indicator may yield a lower limit only if cosmogenic $^{22}\text{Ne}/^{21}\text{Ne}$ is less than about 1.08.

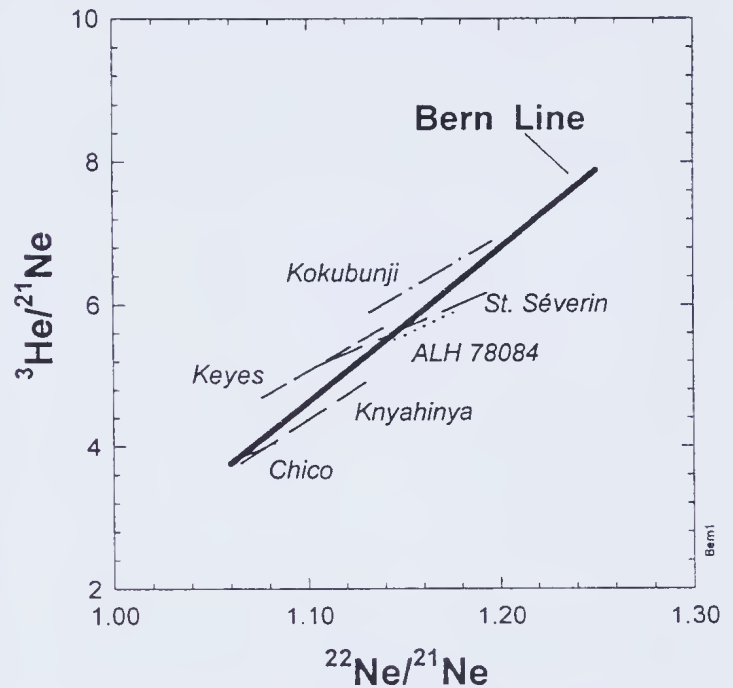


Figure 2. Cosmogenic $^3\text{He}/^{21}\text{Ne}$ versus $^{22}\text{Ne}/^{21}\text{Ne}$ in chondrites. The Bern-Line (Eberhardt *et al.* 1966) is obtained from measurements of different meteorites. Other lines are measurements of samples taken from defined locations within one meteorite or from individual specimens of a meteorite shower (adapted from Loeken *et al.* 1992; references are given therein).

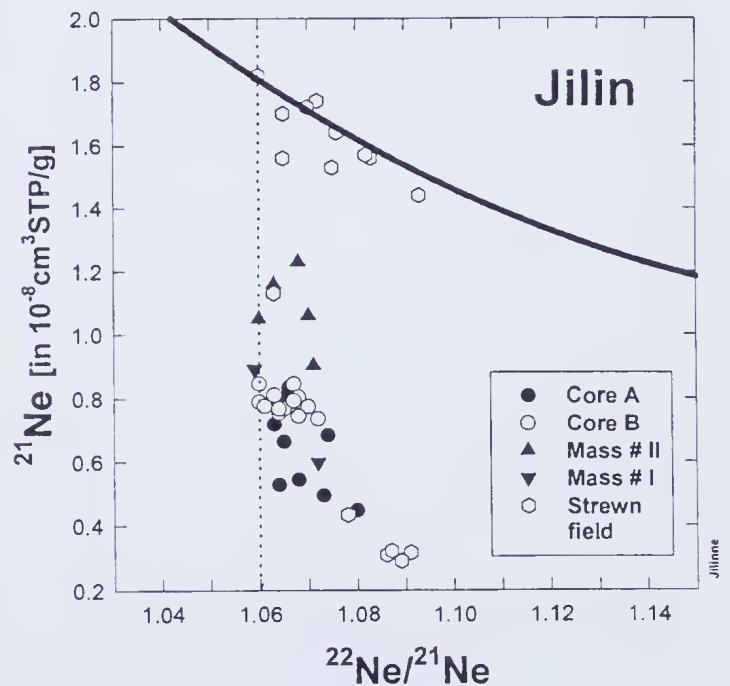


Figure 3. Concentration of cosmogenic ^{21}Ne as function of cosmogenic $^{22}\text{Ne}/^{21}\text{Ne}$ in samples taken from the Jilin chondrite (Begemann *et al.* 1995). The solid curve is the expected trend of the shielding effect on the production rate of ^{21}Ne (Eugster 1988; normalized to $^{21}\text{Ne} = 1.8 \times 10^{-8} \text{ cm}^3 \text{ STP/g}$ and $^{22}\text{Ne}/^{21}\text{Ne} = 1.06$). These measurements show clearly that for $^{22}\text{Ne}/^{21}\text{Ne} < 1.06$ the predicted relation is not valid and that $^{22}\text{Ne}/^{21}\text{Ne} = 1.06$ is the lower limit of cosmogenic neon in chondrites.

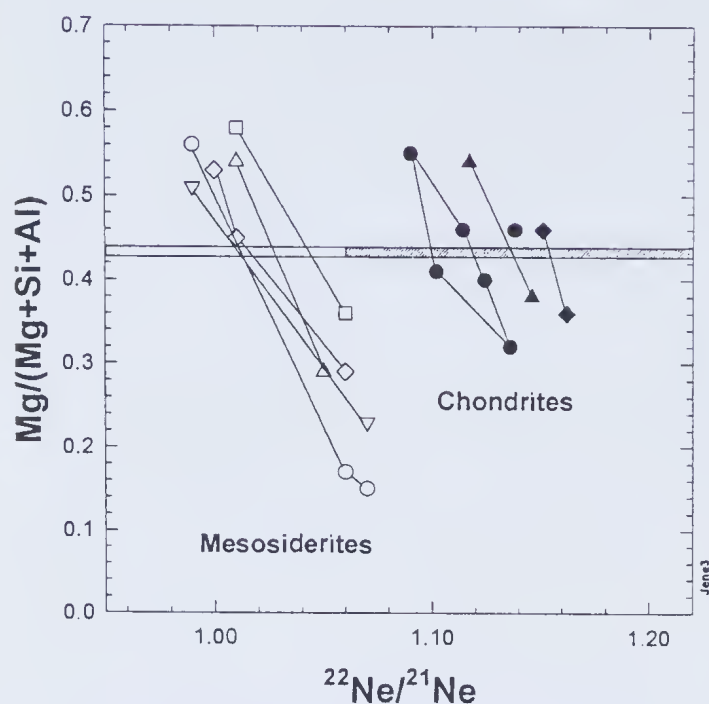


Figure 4. Cosmogenic $^{22}\text{Ne}/^{21}\text{Ne}$ ratios of silicates from chondrites and mesosiderites that have values smaller than 1.06 (adapted from Begemann & Schultz 1988). Data points are connected when different mineral separates from the same meteorite have been analyzed.

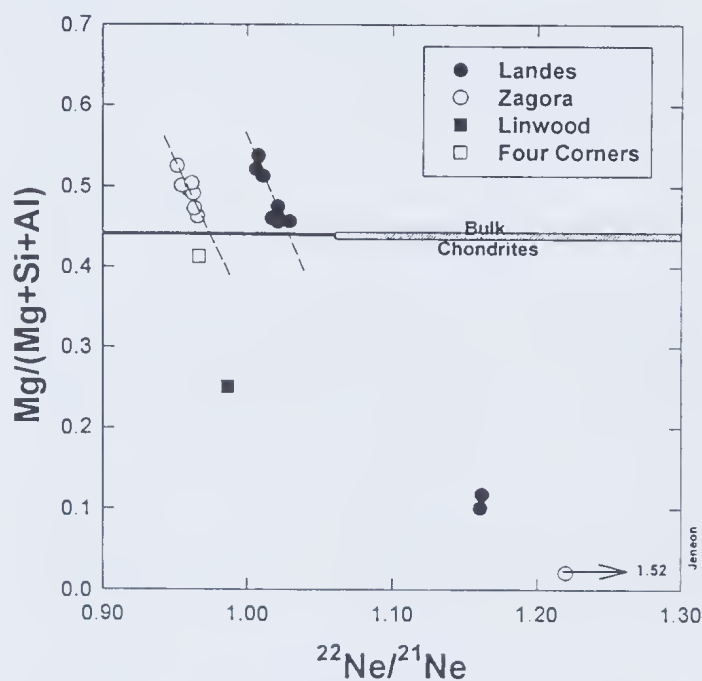


Figure 5. $^{22}\text{Ne}/^{21}\text{Ne}$ ratios of silicate separates from iron meteorites as function of their $\text{Mg}/(\text{Mg}+\text{Si}+\text{Al})$ ratio. The position of chondrites is shown by the hatched area. For the same chemical composition the silicates of iron meteorites have lower $^{22}\text{Ne}/^{21}\text{Ne}$ ratios due to an enhanced flux of secondary neutrons. Samples with low Mg concentrations are feldspar-rich with relatively high sodium contents. Their $^{22}\text{Ne}/^{21}\text{Ne}$ is influenced by higher production rates of ^{22}Ne from Na.

It should also be noted that in the metal phase of iron meteorites, cosmogenic $^{22}\text{Ne}/^{21}\text{Ne}$ is generally greater than 1.06 (see compilation by Schultz & Kruse 1989).

Figure 4 (adopted from Begemann & Schultz 1988) shows $^{22}\text{Ne}/^{21}\text{Ne}$ as a function of the $\text{Mg}/(\text{Mg}+\text{Si}+\text{Al})$ ratio. More than 95% of cosmogenic neon is produced in chondrites under normal shielding conditions from these three elements, about 80% alone from Mg. There is a small dependence of the $^{22}\text{Ne}/^{21}\text{Ne}$ on the chemical composition as indicated by the lines connecting measurements of mineral separates of individual meteorites. Referring to the same chemistry [= $\text{Mg}/(\text{Mg}+\text{Si}+\text{Al})$] the lowest $^{22}\text{Ne}/^{21}\text{Ne}$ of mesosiderites is about 1.01 and definitely lower than the lower limit for chondrites of 1.06.

Figure 5 shows a similar diagram for the measurements of silicate inclusions from iron meteorites. The mineral separates of Landes and Zagora show a similar dependence of $^{22}\text{Ne}/^{21}\text{Ne}$ ratios on chemistry as observed for mesosiderites; however, the feldspar samples do not follow this trend because of the ^{22}Ne produced from Na (see above). The $^{22}\text{Ne}/^{21}\text{Ne}$ - if taken at the chondrite chemical composition - is 1.03 for Landes and 0.97 for Zagora. Those of Linwood and Four Corners cannot be deduced with certainty from this graph because only one sample of each was measured. However, assuming similar relations between chemistry and $^{22}\text{Ne}/^{21}\text{Ne}$ as observed for Landes and Zagora, the cosmogenic $^{22}\text{Ne}/^{21}\text{Ne}$ is even smaller than 0.97.

The underlying physical reason for smaller cosmogenic $^{22}\text{Ne}/^{21}\text{Ne}$ ratios in iron-rich meteorites compared to chondrites is the higher multiplicity for the production of secondary neutrons from high-Z elements like Fe and Ni as compared to Mg, Si or Al (Begemann & Schultz 1988). These additional neutrons enhance the production rate of ^{21}Ne via the reaction $^{24}\text{Mg}(n,\alpha)^{21}\text{Ne}$ and, thus, lower the cosmogenic $^{22}\text{Ne}/^{21}\text{Ne}$ ratios.

This effect complicates their use as a shielding indicator of silicates in iron-rich meteorites because $^{22}\text{Ne}/^{21}\text{Ne}$ depends on the following:

- (1) Chemical composition of the analyzed sample, especially the Mg concentration. This effect is seen by the dashed lines in Figure 5.
- (2) The chemical composition of the bulk meteorite because a high-Z matrix will change the secondary neutron flux. The difference between individual iron meteorites in Figure 5, after taking into account the chemical composition of the minerals, is presumably partly due to their different percentage of silicates, graphite and troilite.
- (3) Shielding as a function of preatmospheric size and location of the analyzed sample.

This complicated relationship makes it difficult to use the cosmogenic $^{22}\text{Ne}/^{21}\text{Ne}$ in silicates separated from iron rich meteorites as a shielding correction factor of cosmogenic nuclide production rates. Furthermore, model calculations or empirical models describing production rates of cosmogenic nuclides in iron meteorites (e.g. Nagai *et al.* 1993) must consider this matrix effect.

Acknowledgments: We dedicate this paper to J de Laeter and we thank him for his continuing interest in our work and for his wise council in many questions concerning atomic weights and isotopic ratios. We thankfully acknowledge the advice of K Rosman in regard to this paper and thank R Clarke for providing meteoritic samples.

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Aspects of low energy nuclear fission

J W Boldeman

Physics Division, Australian Nuclear Science and Technology Organisation, Private Mailbag 1, Menai NSW 2234

Abstract

Since the discovery of nuclear fission in 1939 there have been numerous studies of the fission process. This paper considers several areas of research to illustrate some of the contributions that have been made. The emphasis is on neutron-induced fission at relatively modest excitation energies with some consideration of spontaneous fission.

Introduction

The fission process is defined as the division of a heavy excited nucleus into two fragments similar in mass. Since the discovery of fission (Hahn & Strassman 1939) there have been tens of thousands of research papers devoted to different aspects of the process. The two primary reasons for these extensive studies are obviously the generation of accurate data and understanding of the process for the design and subsequent safe operation of power and research reactors and the contribution that such studies can make to an improved understanding of nuclear structure. Because of the enormous range of topics and the plethora of details, this paper can address at most only a minute fraction of the current literature. The emphasis here will be on low energy neutron induced fission. Over the years there have been many excellent reviews. An extremely comprehensive book by Vandenbosch & Huizenga (1973) covered the studies to that date. A very recent book on the topic was edited by Wagemans (1991). The basis of selection of material for the various figures has been to provide a simple picture of the various processes.

In order to understand what is happening in the fission process, it is clear that there are a number of questions that must be answered. Some of the more obvious are listed below;

- if fission can occur what is it that stops all nuclei from breaking apart spontaneously?;
- what determines the fission probability?;
- when fission does occur what can be learnt from the angular distribution of the fragments?;
- how is the energy shared after fission?;
- what is the mass distribution of the fragments?;
- how are the neutrons emitted in the fission process and what are their energy distribution?; and
- what can be learnt from the yields in the symmetric region of the mass yield curve?

The Fission Barrier

The starting point in any discussion of the fission barrier is the liquid drop model introduced before fission was actually discovered but modified almost immediately by Bohr & Wheeler (1939). In this model, the nucleus is assumed to be equivalent to a liquid drop in which the short range nuclear forces are idealised by the surface tension of the drop and the Coulomb repulsive forces are included by assuming the drop to be uniformly charged throughout its volume. Fission occurs within this model if sufficient excitation is given to the system to allow the internal vibrations to overcome the attractive surface tension of the drop. Although the liquid drop model provided, in principle, a reasonable approximation to the real world, it failed in accurately predicting many of the detailed systematics of the fission process.

A major advance occurred in the mid 1960's, when the model was improved dramatically by the inclusion of shell effects (Strutinsky 1967; Strutinsky & Pauli 1969). The consequence of these corrections is illustrated by plotting the potential energy hindering fission as a function of the symmetric axis deformation (Fig 1); also shown is the smooth potential barrier as originally predicted by the liquid drop model. It is seen that the single smooth barrier of the simple liquid drop model becomes double humped for nuclei in the vicinity of the uranium. This extension of the model allows many unexpected features of the fission process to be explained. It also explains why the ground state for those nuclei represented by the potential barrier in the figure (nuclei in the vicinity of the uranium nuclei) is deformed.

It is now important to introduce the concept of fission channels. In 1956, A Bohr first suggested that for a fissioning nucleus with excitation only slightly more than the fission threshold *i.e* with an energy only slightly exceeding the potential energy barrier in Fig 1, the nucleus at a deformation corresponding to the highest point in Fig 2 is cold with respect to internal excitation, all energy is bound up in potential energy of deformation and the only nuclear states at the peak of the fission barrier (the saddle point) via which fission can proceed will be collective states similar to those of the heavy deformed nuclei near their ground states *i.e* in the first well of the potential barrier in Fig 1. The transition states will be characterised by the quantum numbers l and K , where l is the total spin of the compound nucleus and K is its

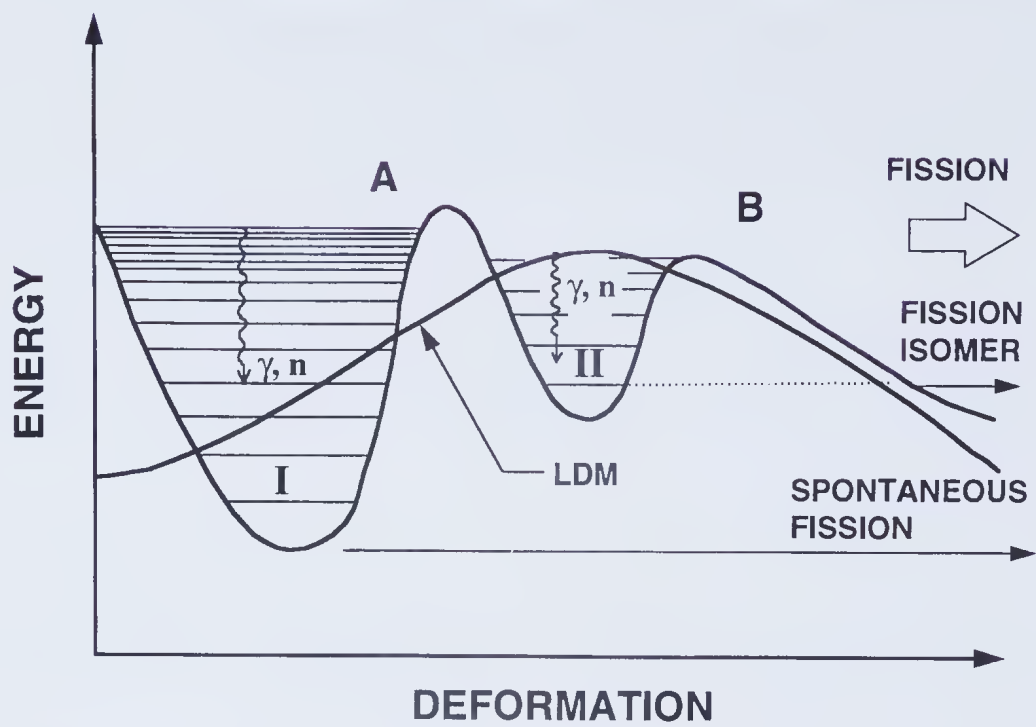


Figure 1. Double humped fission barrier, compared with the liquid drop model (modified from Strutinsky (1967)).

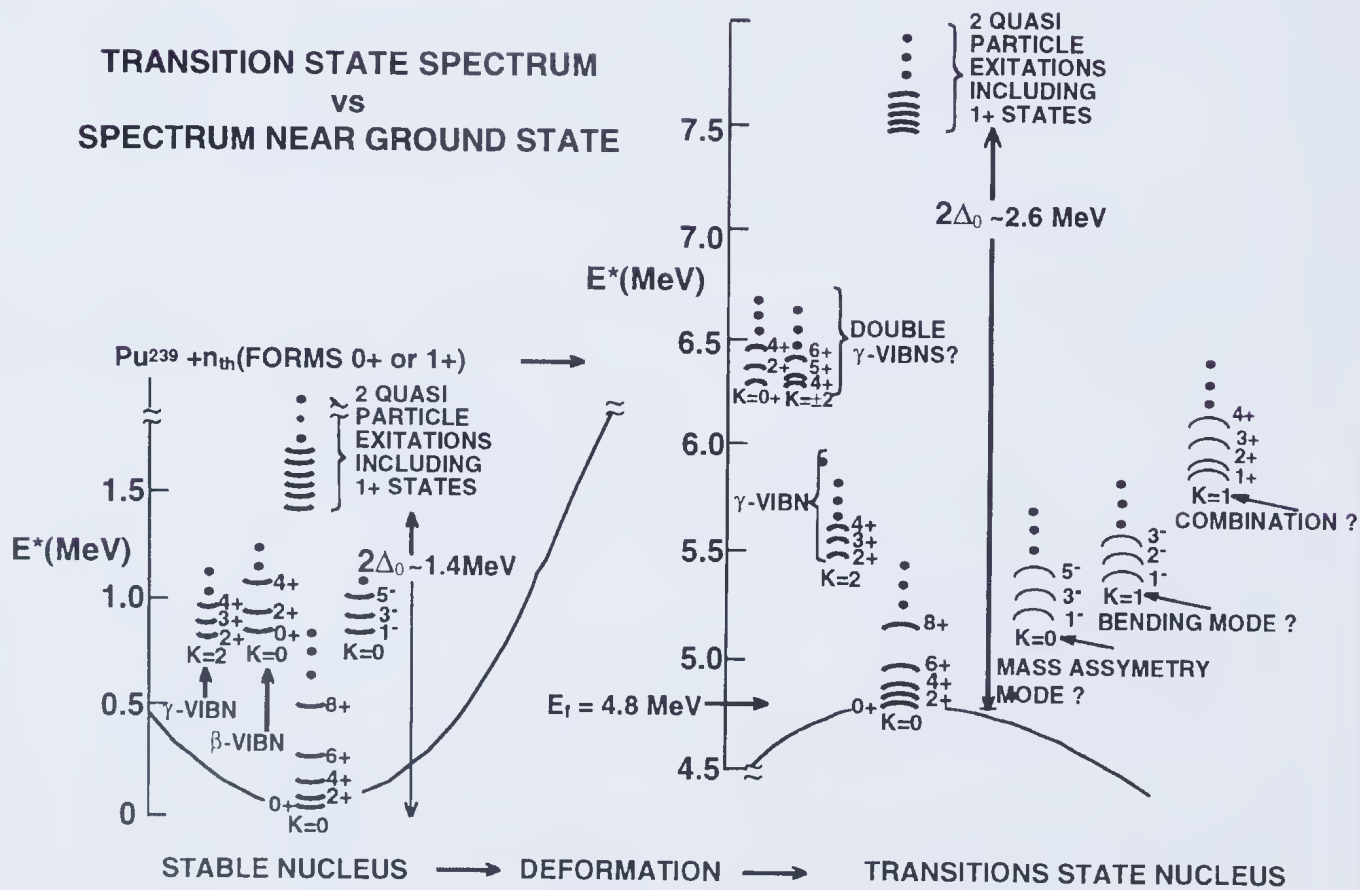


Figure 2. Comparison of transition states at the fission barrier with the spectrum of low lying states for deformed nuclei (modified from Griffin 1965).

projection on the symmetric axis *i.e.* along the axis of deformation specified by the deformation parameter in Fig 1. Extensive research, particularly in the early days of fission studies, identified a spectrum of different quantum states at the saddle point which were necessary to explain many of the details of the fission process. Figure 2, modified from Griffin (1965) illustrates the wealth of data that has been obtained principally from studies of fission fragment angular distributions. Although this information was derived originally for a simple single humped barrier, to a first approximation Fig 2 represents the spectrum of double humped transition states.

As indicated previously, the angular distribution of the fission fragments can be used to derive information regarding the spectrum of states at the saddle point of the fissioning nucleus (Fig 2). In an even-even nucleus, the spectrum of transition states at the saddle point deformation is expected to be quite similar to that found at low excitation in its permanently deformed equilibrium configuration. The ground state has total angular momentum and parity $I\pi = 0+$ and has projection of angular momentum on the nuclear symmetry axis $K = 0$. The excited states correspond to the simple vibrational modes of a liquid drop. The lowest mass-asymmetric mode has $K = 0$, but negative parity, whereas the axial-symmetric gamma vibration of lowest energy has $K\pi = 2+$. In addition, a bending mode with $K\pi = 1-$ is expected to occur at moderate excitation at the saddle point, although it has not been identified at equilibrium deformation. Since the fissioning nucleus is non-spherical, rotational bands of increasing I are built on each of these vibrational states. Simple superposition of these fundamental modes leads to further fission channels with increasingly greater excitation until, at about 1.5 MeV, sufficient energy is available to break nucleon pairs and thereafter single particle

excitations combined with collective vibrations lead to a rapid increase in the complexity of the transition state spectrum.

Fission Fragment Angular Distributions

A basic assumption of the Bohr model is that the quantum number K remains a constant of the motion between saddle point and scission. Thus the measured angular anisotropy $W(0^\circ)/W(90^\circ)$ can be used to provide information on the properties of the transition states at the saddle point. The most extensively studied even-even fission system studied is neutron fission of ^{235}U . Figure 3, modified from the recent study by Straede *et al.* (1987) shows the anisotropy *i.e.* $W(0^\circ)/W(90^\circ)$ as a function of neutron energy. The data is readily explained in terms of the model discussed above.

For neutron fission of an even target nucleus leading to an odd fissioning system, the lowest lying fission channels are expected to be essentially single particle states which should be identifiable with the appropriate Nilsson orbits. The excess angular momentum appears as a rotation about an axis perpendicular to the symmetric axis. Thus with each intrinsic state there is associated a rotational band with energy given by

$$E(I\pi) = E_0 + \frac{\hbar^2}{2J} [I(I+1) - 2K^2 + \delta_{K \neq 1/2} \alpha(-1)^{I+1/2} (I+1/2)] \quad (\text{eq. 1})$$

where J is the moment of inertia associated with the band and α is the decoupling constant for the $K = 1/2$ bands. The structure in the anisotropy becomes much larger. As an example, measurements of the anisotropy for neutron fission of ^{230}Th near the large resonance in the cross section at 715 keV are shown in Fig 4.

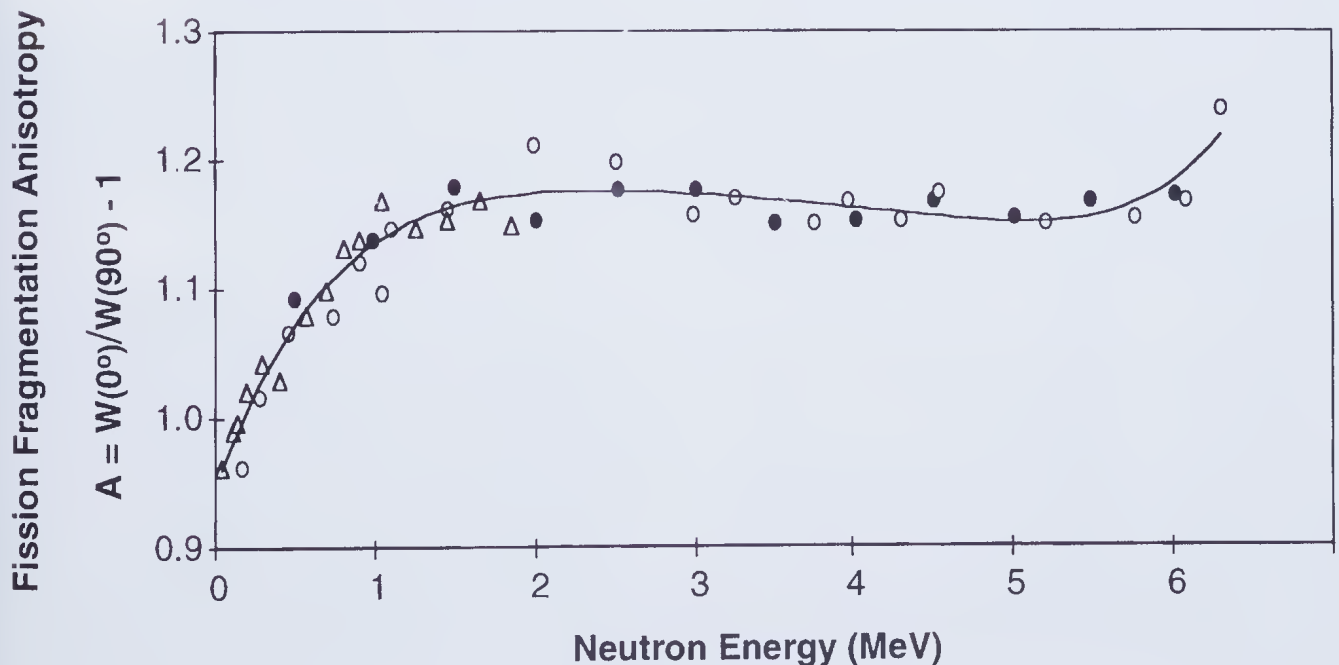


Figure 3. The $^{235}\text{U}(n,f)$ fission fragment anisotropy (modified from Straede *et al.* 1987).

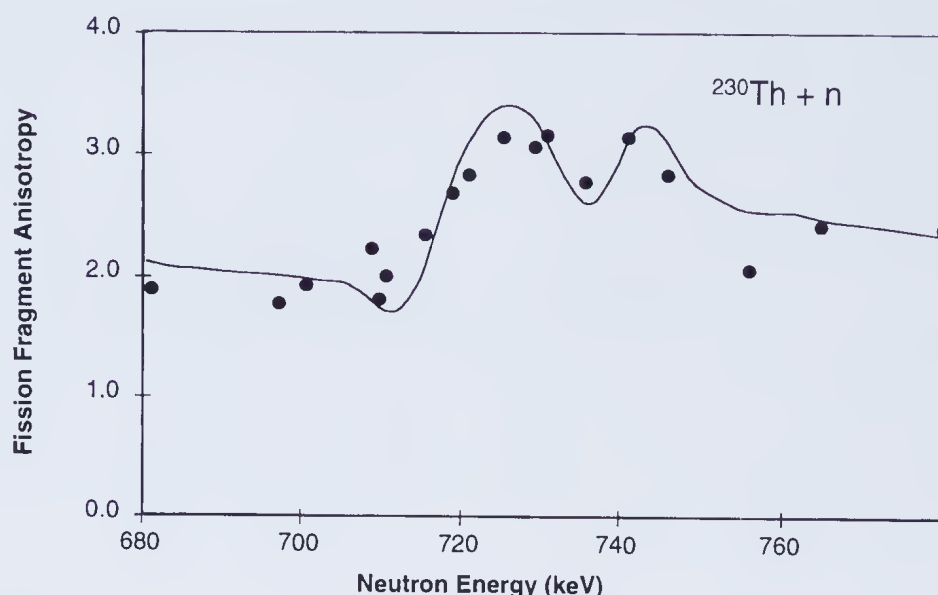


Figure 4. Fission fragment anisotropy¹⁰ for neutron fission of ²³⁰Th (adapted from Boldeman & Walsh, 1986).

Sub-barrier Fission Cross-sections

For nuclei represented by the fission barrier in Fig 1, fission can only take place if sufficient energy is given to the system to allow it to proceed either over the barrier or to tunnel through. For sub-barrier fission, the cross section is given by an expression which contains reaction information multiplied by the penetrability through the barrier. The penetrability through the simple liquid drop fission barrier is given by the expression

$$P_i = [1 + \exp(2\pi(E_i + E^{IK\pi} - E)/\hbar\omega_i)]^{-1} \quad (\text{eq. 2})$$

where E_i is the height of the barrier, $E^{IK\pi}$ is the energy of level $(IK\pi)$, E is the excitation energy and $\hbar\omega$ is the curvature of the fission barrier. With a double humped barrier the expression becomes a little more complex

$$T_i^K = t_K + (1 - r_K - t_K) P_A(P_A + P_B) \quad (\text{eq. 3})$$

where t_K and r_K are the transmission and reflection coefficients which relate to the amplitudes of the fission wave functions inside and outside the nuclear potential

and P_A and P_B are the penetrabilities for the two barriers defined as before.

Some unexpected features of the fission cross-section follow from the double humped barrier shape. The potential well between the two humps of the double humped barrier will clearly contain states similar in character to the states in the first well. However the level density at a specific excitation will be different because of the different heights above the ground state. This produces some interesting structure in the sub-barrier cross-section. Figure 5, adapted from Migneco & Theobald (1968), illustrates the influence of the coupling of states in the first well to states in the second well. The gross structure in the sub-barrier neutron fission cross section of ²⁴⁰Pu reflects the spacing of levels in the second well of the fission barrier while the fine structure is related to the level density in the first well.

Although many nuclei have barrier shapes characterised by the doubled humped shape of Fig 1, it was predicted by Moller & Nix (1974) that, if asymmetric

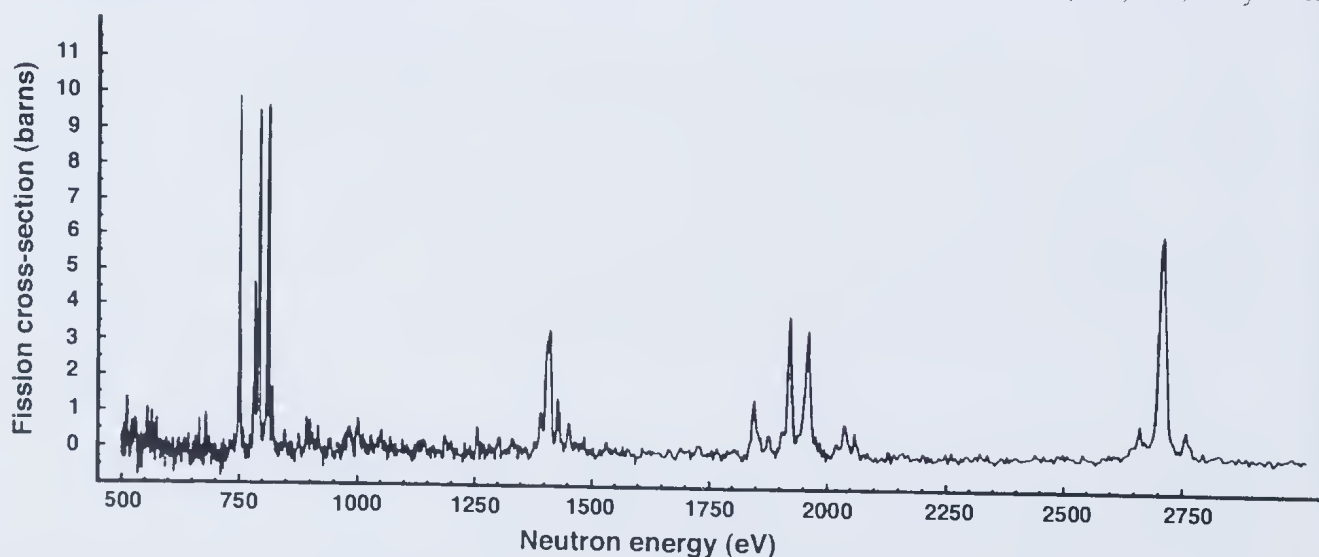


Figure 5. The neutron fission cross section of ²⁴⁰Pu between 500 eV and 3000 eV (adapted from Migneco & Theobald 1968).

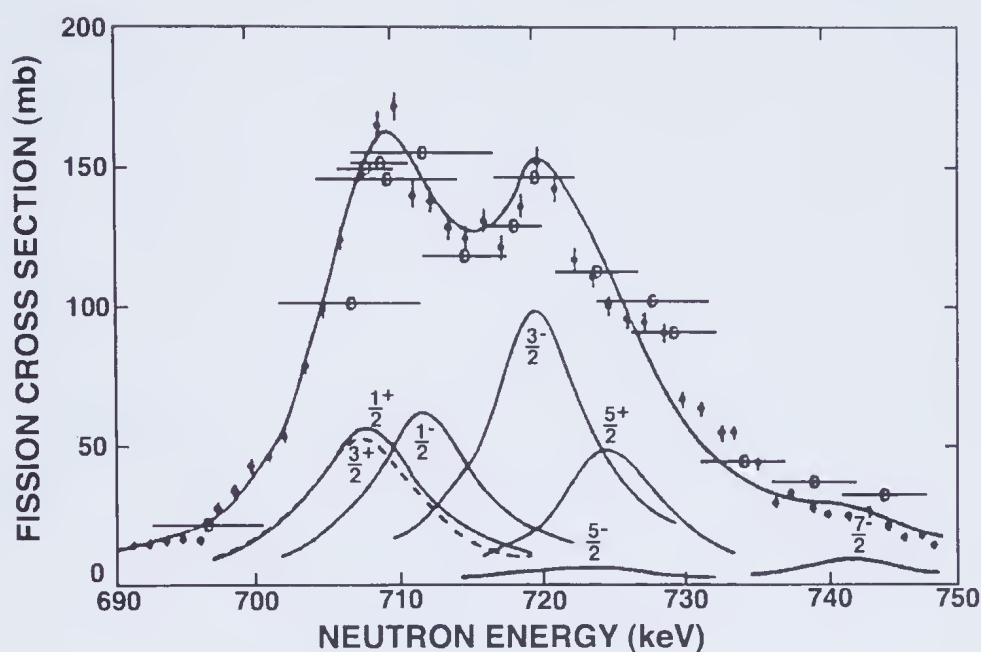


Figure 6. Calculated neutron fission cross section compared with the experimental data of Blons *et al.* (1978). Also shown are the fission cross section data from the angular distribution measurements (Boldeman & Walsh 1986).

deformations are taken into account for nuclei in the vicinity of thorium, then the second barrier should itself split into two separate peaks making the barrier triple humped in character. The consequences of this characteristic are shown in the sub-barrier neutron fission cross section of ^{238}U as measured by Blons *et al.* (1978). The broad sub-barrier resonance in the cross-section at 715 keV is interpreted as fission through a pure vibrational state in the third well of a triple humped fission barrier. Some controversy regarding the detailed interpretation of the data exists. One interpretation (Boldeman & Walsh 1986) involving a simultaneous fit to the cross section in Fig 6 and the anisotropy data in Fig 4 is presented below.

Fission Fragment Yields and Associated Neutron Emission

One of the most extensively studied aspects of the fission process has been the systematics of the mass division. In this context, it is important to distinguish between the fission fragments and fission products and ultimately accumulated product yields. At the instant of scission, the two fission fragments are highly deformed with a high level of internal excitation, although a large proportion of the energy emitted in fission is contained in the kinetic energy of the fission fragments resulting from Coulomb repulsion. Since the fragments are neutron rich with respect to the stability line, this deformation energy is emitted primarily by neutron evaporation and by prompt gamma emission. The term fission products is used to describe the resulting nuclei. Such nuclei are still radioactive and undergo further radioactive decay leading to what are called cumulative yields. Figure 7 illustrates the well known asymmetric division that is typical for low excitation neutron fission of nuclei near

uranium (modified from Wahl 1965). The dominating influence in the determination of the shape of the curve is the existence of the magic number $N=50$ at mass 80 on the lower end of the distribution and the doubly magic nuclei $Z=50$, $N=82$ in the vicinity of mass 128. It is also known that the symmetric region between the two peaks of the mass yield curve starts to fill as the excitation increases. This can be explained quite simply as the reduction of shell effects as the excitation energy increases. Neutron emission from the individual fission fragments is a function of the mass of the fragment (Fig 8; from Nifenecker *et al.* 1973). The resulting "saw tooth" shape of the neutron emission is also consistent with the explanation presented above. The minimum in the saw tooth curve occurs in the vicinity of the closed shell nuclei. These nuclei are stiff with respect to deformation and therefore less deformation occurs in these fragments. On the contrary, near the peak of the neutron yield curve, the fragments are soft with respect to deformation and a larger proportion of the total fission energy is involved in the deformation of these fragments.

Fission Product Yields in the Symmetric Region

Studies of fission product yields in the symmetric region for thermal neutron fission of the uranium nuclei are important for at least three reasons. Although the yields are low, in a power reactor significant masses of such nuclei are produced and the management of the reactors requires this knowledge. A second reason follows from suggestions of fine structure in the fission fragment/(product) yields. The symmetric region provides an opportunity to carry out such studies since there are several elements with large numbers of isotopes (*e.g.* Sn) which therefore simplifies the chemistry. In addi-

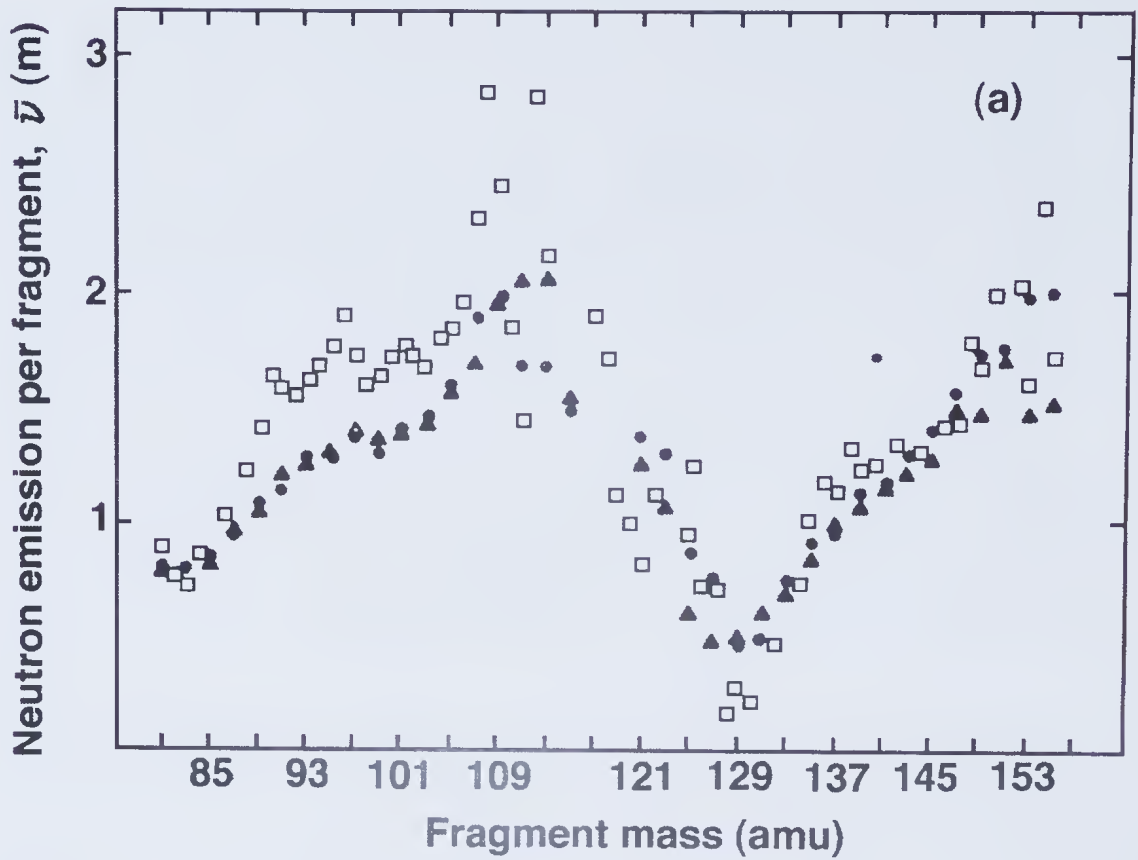


Figure 7. Fission product yields¹⁴ for thermal neutron fission of ^{233}U , ^{235}U and ^{240}Pu and spontaneous fission of ^{252}Cf (from Wahl, 1965).

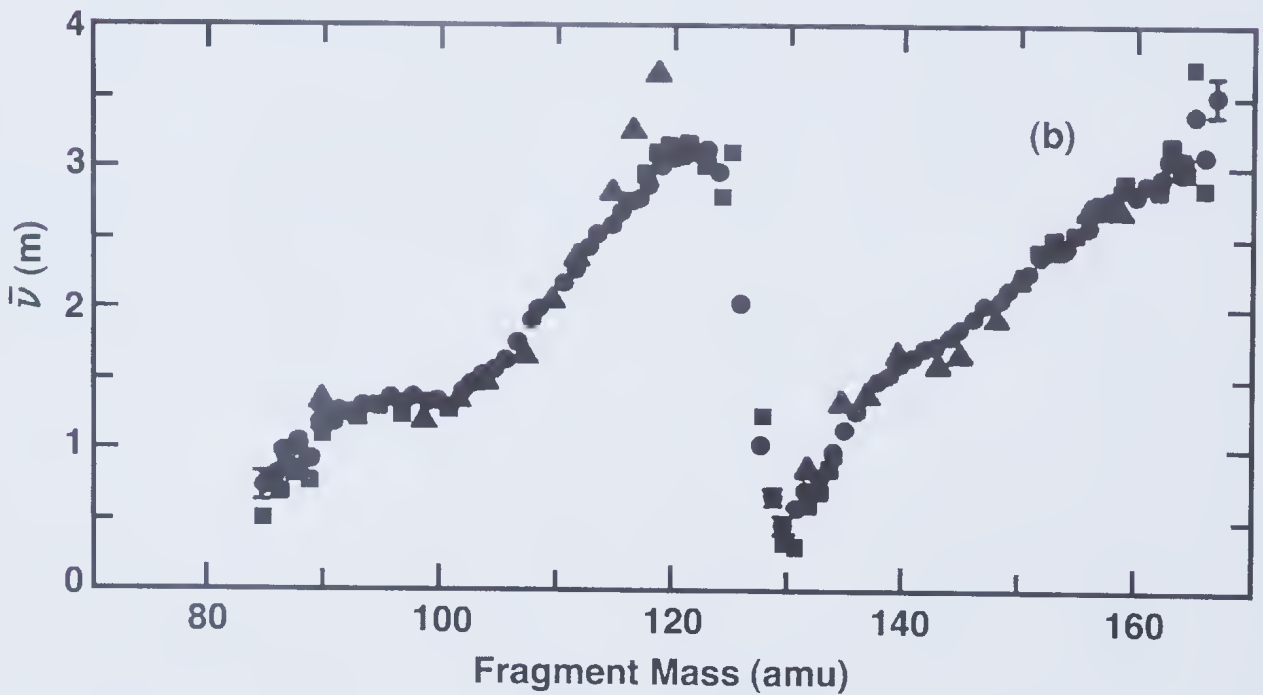


Figure 8. Average neutron emission per fragment as a function of fragment for (a) thermal neutron fission of ^{235}U and (b) spontaneous fission of ^{252}Cf (from Nifenecker *et al.*, 1974).

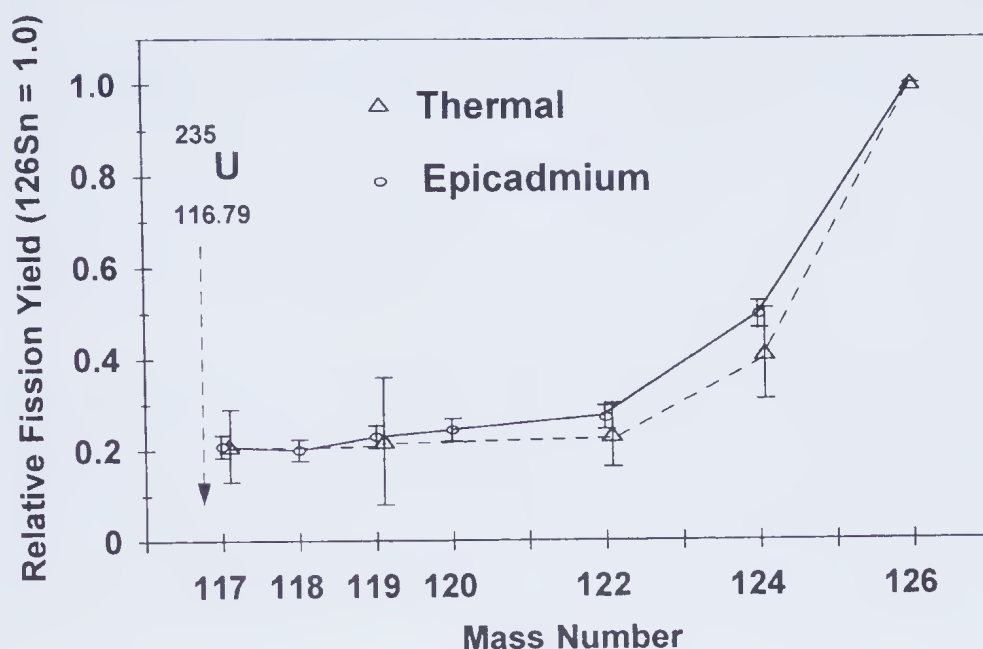


Figure 9. Relative fission yields for isotopes of tin for neutron fission of ^{235}U (thermal and epithermal) normalised to ^{126}Sn (from Rosman *et al.* 1986).

tion, there are extensive studies of earth science where spontaneous fission of the uranium nuclei produce elemental contaminations that need correction. A series of studies by Rosman *et al.* (1983) has produced considerable symmetric mass yield data. Figure 9 shows their data for the Sn isotopes in the symmetric mass yield region; an absence of fine structure is apparent.

Recent Developments of the Theory

In very recent times, there have been some important developments of the theory of fission particularly at low excitation. These developments have been summarised by Brosa *et al.* (1990). Effectively, they involve a more complete consideration of the later stages of the process effectively from the saddle point to scission. These new discoveries show that for low excitation fission there are several exit channels on paths to scission. Furthermore, when the nucleus is close to scission there is some randomness in where the neck connecting the elongated nucleus may actually rupture. These considerations are beyond the context of this paper and the reader is referred to Brosa *et al.* (1990) and other papers mentioned in that text.

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Isotopic studies of the Oklo fossil reactors and the feasibility of geological nuclear waste disposal

R D Loss

Department of Applied Physics, Curtin University of Technology, Perth, WA 6102

Abstract

In 1972, six 2000 million year old natural fossil nuclear fission reactors were discovered at a uranium orebody at Oklo in Gabon, South West Africa. Over a period of about one million years the reactors produced some hundreds of tonnes of fission products with characteristic but unnatural isotopic compositions. These isotopic compositions have enabled the nuclear characteristics of the reactors and the extent to which they have retained their fission products to be determined. Since their discovery another dozen fossil fission reactors have been found in Gabon. This paper summarizes the results obtained from both the earlier and recent discoveries and their implications for the storage of anthropogenically generated fission waste in geological environments.

Introduction:

The existence of natural fossil chain fission reactors is perhaps one of the most unusual discoveries in the comparatively short history of nuclear science. When Fermi and colleagues initiated the first artificial self sustaining chain fission reactions they did not realize that nature had assembled and operated a similar type of reactor 2000 million years before. Fourteen years after Fermi's achievements, Kuroda (1956) published the details of the conditions under which such reactors could exist. However, despite an extensive survey of the $^{235}\text{U}/^{238}\text{U}$ ratio during the 1960s, no variation greater than analytical uncertainty ($\pm 0.1\%$) was found. In 1972, routine measurements of $^{235}\text{U}/^{238}\text{U}$ in a French uranium processing plant revealed a depletion in this ratio of 0.43%. At first it was thought that this was caused by "spent fuel" from a conventional fission reactor but it was eventually traced to uranium from a sedimentary type uranium deposit at Oklo in Gabon, South West Africa. A survey of the existing Oklo mine site revealed six metre long and tens of centimetres thick lenses of highly enriched U which contained both depleted $^{235}\text{U}/^{238}\text{U}$ ratios and substantial quantities of nuclear fission products. The circumstance giving rise to these fossil nuclear reactors has subsequently become known as the "Oklo Phenomenon".

The potential significance of the Oklo fossil reactors as natural analogs for geological repositories of radioactive waste was quickly recognized by the scientific community. Although the possibility of geological storage had been considered prior to the discovery of the Oklo reactors, the methods of assessing waste retention over the time required for it to decay to "safe" levels were extremely limited. The long term behaviour of such waste had to be extrapolated from extremely short term experiments under conditions which poorly approximated those likely to be found in real repositories. Direct experimentation of sites through trial deposition of hun-

dred of tonnes of fission waste was also potentially environmentally irresponsible. Besides, the waste problem needs to be tackled now and cannot wait for the time required to assess the potential of geological storage.

The role of isotopic studies:

Isotopic studies have proved to be the master key for unlocking the many secrets of the Oklo phenomenon. Although non-isotopic studies of the Oklo reactors may reveal unusual amounts of some elements it is only by measuring their isotopic composition that the existence of nuclear fission can be confirmed. Isotopic studies by mass spectrometry are especially powerful because they allow the fission products to be distinguished from the natural elements and their amounts measured in any rock sample.

The wealth of information available from isotope studies can be illustrated using tellurium as an example. Figure 1 shows the relative isotopic compositions of five of the major isotopes of tellurium as measured in a range of samples. For comparison all isotope abundances are referenced to the ^{130}Te abundance taken as unity. The solar system values shown are those present in all terrestrial sources, meteorites and the moon (Smith et al., 1978). Samples ORZ9-028 and ORZ9-006 represent Te from samples from inside reactor zone 9 while OHR9-002 is from a host rock sample taken 1.4 m away from this reactor zone.

The isotopic abundances of ^{128}Te and ^{130}Te in ORZ-028 are essentially the same as that produced by the fission of ^{235}U . Since no ^{124}Te is produced by fission, the absence of this isotope indicates that no terrestrial Te is present in the reactors and that all of the Te present in the reactors is fissionogenic. The ^{128}Te abundance in OHR9-002 indicates that this sample contains a mixture of both fissionogenic and solar system Te. The other isotope of significance is ^{126}Te which is in excess in samples ORZ9-006 and in particular OHR9-002. This effect arises from the parent isotope, ^{126}Sn which has a half life 10^5 years indicating that radioactive tin is mobilized inside and in the immediate

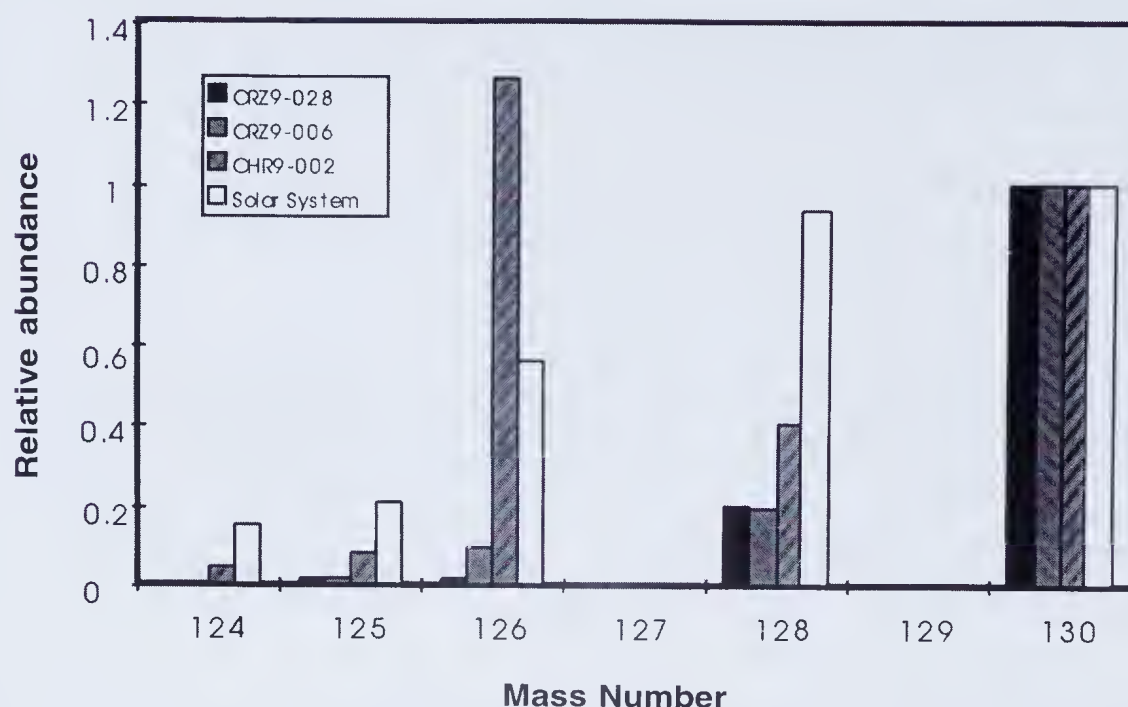


Figure 1. The isotopic composition of tellurium in a range of Oklo and other samples (data from Curtis *et al.* 1989 and Loss *et al.* 1989)

vicinity of the reactors during the reactions and within one million years (10 half lives) of the last reaction. The abundance of fission product Te present in OHR9-002 was also measured to be 3 orders of magnitude lower than that in the reactor zone while at a distance of six metres from the reactor zone the abundance of fission product Te is 1 part in 10^5 of that inside the reactors.

Besides confirming the occurrence of the fission process at Oklo, the isotopic compositions of the fission products enabled the nuclear characteristics of the reactors themselves to be determined (Naudet 1975 and Ruffenach *et al.*, 1980). The parameters of interest include the integrated neutron flux (fluence), the degree of thermalization of the neutron spectrum, and the fractional fission contribution from ^{238}U and ^{239}Pu . From these parameters, other physical characteristics such as the power output and temperature of the reactors and surrounding host rocks can be determined. These parameters, together with the age of the reactors, the degree of U enrichment and other geochemical parameters have been used to calculate the total quantity of fission products expected to be produced by the reactors. When this is compared to what is present today a retention factor for the fission products can be determined. For example, reactor zone 9 has retained more than 80% of its fissiogenic Te - a remarkable achievement for a 2000 million year old uranium oxide mineral assemblage located inside a highly porous sandstone matrix.

Isotopic studies have shown that many fission produced elements have been retained inside the reactor zones (Curtis *et al.*, 1989). The rocks surrounding the reactors have also retained other fission products within a few metres of the reactor zones (Loss *et al.*, 1989). These results are in excellent agreement with those predicted by thermodynamics and geochemistry (Brookins, 1975). However, there are still many aspects of the reactors that remain to be studied.

Recent discoveries

Since 1972, another dozen or so fossil fission reactors have been discovered at Oklo, Oklobondo and at Bangombe, some 30 km further south of Oklo. These reactors are significant discoveries in their own right since they include a wider range of geological conditions than those represented by the original reactors. One of these reactors is located within metres of a 1000 million year old doleritic dike which cut through the centre of the Oklo uranium ore deposit. This has provided the opportunity to study the affect of dike emplacement on the retention of fission products within a reactor. Although only a limited number of studies of these newer reactors have been undertaken the retention of fission products appears to be similar to those for the original reactors. Amongst the most significant new results has been the detection of previously unstudied but very important long lived radiogenic and highly mobile nuclei, ^{137}Cs (decaying to ^{137}Ba) and ^{90}Sr (decaying to ^{90}Zr) within metres of reactor zones. These elements were previously thought to have been completely lost from the vicinity of the reactors (Hidaka *et al.*, 1993 and 1994). Another unusual discovery has been the formation of unusual refractory and highly insoluble alloys which have trapped almost pure fissiogenic elements within the original uraninite ore grains (Gauthier-Lafaye *et al.* 1996). Studies of this type of alloy may prove useful in developing a suitable storage matrix for some types of spent fuel.

Perhaps the most unusual of the new reactors are those at Bangombe which are much closer to the surface and considerably more weathered and oxidized than those at either Oklo or Oklobondo. Studies of this type of reactor will be particularly useful since future underground waste sites may eventually be exposed to surface conditions and more aggressive geochemical environments. Isotopic studies of minerals within and surrounding this reactor zone has identified clays and phosphates

as important in retaining rare earth element fission products. A case in point is the detection plutonium retention identified by a higher than solar system $^{235}\text{U}/^{238}\text{U}$ ratio (Bros *et al.* 1993). This has occurred in what has essentially been a high rainfall equatorial environment for perhaps millions of years.

Conclusions

The most important lesson that Oklo teaches us is that nature is able to isolate fissiogenic waste in geological environments for extremely long periods of time even though the reactors were contained in a highly fractured, porous and physically "leaky" matrix. This geophysical environment is one that would hardly be considered as ideal for a nuclear waste repository. The reason for the retention of fissiogenic materials under these conditions was largely due to the local geochemical conditions. The oxidizing potential and acidity of the ground waters together with the presence of scavenging clays and other minerals played a critical role in this process. However it can be concluded that the concept of multiple barrier geological containment including iron oxides and clays which are able to buffer possible changes in ground water conditions indicates that the effective containment of man-made nuclear waste is feasible.

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Isotopic signatures: An important tool in today's world

D J Rokop, D W Efurd, T M Benjamin, J H Cappis, J W Chamberlin,
H Poths, & F R Roensch

Chemical Science and Technology Division, Los Alamos National Laboratory,
MS J-514, Los Alamos, NM 87545 USA

Abstract

High-sensitivity, high-accuracy actinide measurement techniques developed to support weapons diagnostic capabilities at the Los Alamos National Laboratory are now being used for environmental monitoring. The measurement techniques used are thermal ionization mass spectrometry, alpha spectrometry, and high resolution gamma spectrometry. These techniques are used to address a wide variety of actinide inventory issues; environmental surveillance, site characterizations, food chain member determination, sedimentary records of activities, and treaty compliance concerns. As little as 10 femtograms of plutonium can be detected in samples, and isotopic signatures determined for samples containing sub-100 femtogram amounts. Uranium, present in all environmental samples, can generally yield isotopic signatures of anthropogenic origin when present at the 40 picogram g^{-1} level. Solid samples (soils, sediments, fauna, and tissue) can range from a few particles to several kilograms in size. Water samples can range from a few mL to as much as 200 L.

Introduction

The moratorium on weapons testing has made it necessary to find new applications for the radiochemical diagnostic capabilities of the Chemical Science and Technology Division at Los Alamos. Many were explored, but the three which seemed to hold the highest potential for doing both good science and having sufficient funds to support them were environmental monitoring of actinide elements in support of clean-up efforts, providing tracers for industrial applications, and supporting the International Atomic Energy Agency (IAEA) in its efforts to monitor the Non-Proliferation Treaty (NPT). We are actively involved in the first and third areas and aggressively pursuing the second.

Environmental actinide monitoring has historically been done with inexpensive survey techniques, principally alpha spectrometry (AS). The technique, which is fast and relatively simple, suffers one major drawback; it has inadequate resolution to separate anthropogenic source terms from natural background or fall-out. AS also cannot attribute single versus multiple source terms. Mass spectrometric isotopic dilution (MSID), a tool long used by isotope geologists and the nuclear industry, had not until recently been applied in a broad way to environmental problems. Our first effort using this method was an actinide inventory of the Pajarito Plateau, the area surrounding the Los Alamos National Laboratory (LANL). The method quickly illuminated and expanded the scope of actinides in the environment. Actinide concentrations, previously found to be below health limits and therefore not requiring remedial action or attribution, can now be detected with 100 to 1000 times more

sensitivity than historic techniques and can frequently be attributed to a specific source. While this capability is a powerful new tool for environmental researchers, helping determine transport phenomena and remediation effectiveness, it has also created a communication problem of enormous magnitude. How do you explain to concerned citizens, with little scientific background, the tremendous sensitivity of the method, while assuring them of the corresponding negligible health impact?

The nature of any material processing, including nuclear, causes minute amounts of various constituents to be lost during handling. For example, certain fission products, such as Ru, I, and Tc, have very volatile chemical forms which are difficult to contain. Their detection can provide significant information about the processing nature. The large volume of the material potentially handled by proliferants makes actinides and the associated fission products easy to detect. For this reason, the IAEA has decided to adopt environmental monitoring techniques to assist inspectors in assessing member countries compliance with the NPT and other applicable treaties. A former LANL staff member is in Vienna to help the IAEA build a clean laboratory suitable for environmental measurements. An ongoing program is training chemists and mass spectroscopists from the IAEA in low level environmental measurement techniques. LANL also participated, along with other laboratories, in field trial experiments which were used to demonstrate the merits of the MSID method. LANL is expecting to participate, along with other network laboratories, in the forthcoming environmental monitoring program.

This paper will describe the physical requirements necessary to apply the MSID actinide method at environmental levels, the actinide measurement sensitivities of MSID, and specific applications in various matrices.

Clean chemistry and mass spectrometry

A 1400 m² clean chemistry and mass spectrometry facility was built at Los Alamos to accommodate the processing of samples for weapons diagnostics. This facility permits very small samples of the actinides to be handled such that the integrity of the field sample can be protected from contamination to very low levels. Plutonium process blanks are $<3 \times 10^{-15}$ grams and uranium blanks $<1 \times 10^{-9}$ grams. This facility has the capacity to handle >2000 actinide samples annually at this low blank level. Laminar flow "clean" air passed through hepa-filters directly over work surfaces and rigid protocols for sample content and handling help provide this integrity. A complete description of these techniques can be found in several publications (Efurd *et al.* 1992,1993; Rokop *et al.* 1982).

Because of its high crustal abundance, $\approx 3 \times 10^{-6}$ g g⁻¹, natural U in the environment dilutes anthropogenic source terms and makes U a high accuracy measurement. An anthropogenic source term is detected by slight changes to the 235/238 ratio (natural ratio is 0.007254) and the presence of ²³⁶U. Plutonium, on the other hand, occurs at extremely low concentrations and requires a high-sensitivity measurement. Almost all surface material now contains fallout plutonium in the 10-50 femtogram per ≈ 20 g soil sample range. The 240/239 ratio for fallout is subject to slight changes from local signature overlay. The area near Denver, Colorado, with Rocky Flats providing the local overlay, has a 240/239 fallout ratio of 0.169 ± 0.005 (Efurd *et al.* 1994) while sediment samples collected from the Irish Sea have a 240/239 ratio of 0.24 ± 0.01 (unpublished observations; Efurd *et al.* 1995). The integrated average world-wide ratio is 0.18 (Krey, *et al.* 1976).

Given "clean" chemistry and mass spectrometric capability, there are two different philosophies for making measurements if the goal is detecting undeclared or illicit activity. These are the "bulk" and "particle" methods. The "bulk" method involves total dissolution of the matrix or leaching the desired material from the matrix followed by chemical purification and TIMS. The "particle" method involves collecting particles on swipes or filters, separating the particles and depositing them on a slide with collodian, irradiation in contact with Lexan (for recording the fission tracks created by actinide particles) reregistering the slide and lexan, cutting out the desired particle, and, finally, TIMS. While the "particle" method generates less ambiguous results and has little or no background from natural or fallout sources, it is slow, much more expensive (5x) and highly labor intensive. It also suffers from difficulty at trying to sort out the particular or desired indicator of process. IAEA field trials also demonstrated a lower percentage of "hits" (positive response of anthropogenic origin) than "bulk" (integrated, analysis of entire sample). The best situation would utilize the "bulk" method and if a "hit" was recorded and less ambiguity was desired, this would be followed up with the "particle" method.

As more data is gathered from environmental samples, the question of how to interpret the results is becoming very important. LANL uses algorithms developed for weapons diagnostics to separate multiple actinide sources. We plan to work with the IAEA to refine

these models and make them more useful for their specific purposes.

Table 1 lists a selection of some of the different matrices analyzed by the Chemical Science and Technology Division (Los Alamos National Laboratory) for determining environmental actinides. While this list is incomplete, it serves to indicate the wide application of "bulk" analysis. Particularly effective are filter papers of swipes taken from non-technical areas of nuclear facilities; these give almost complete indication of the process nature.

Table 1

Examples of sample materials for which environmental actinide determinations have been made.

NTS Debris	
Soils	
Sediments	
Sea Water	
Fresh Water	
Filter Papers	
Vegetation	pine needles
	grass
	apples
	feces (sheep)
Soft Tissues	whale liver
	whale blubber
	star fish
	salmon
	chubs
	trout
Bones	

Table 2 shows the measurement sensitivities of the MSID "bulk" analysis method. It can be seen that approximately 1000 times more sample is needed for a signature than is required for detection. A caveat here is that recent chemical purification improvements would indicate a lowering of atoms needed for signature by $\sim 10\times$. A general rule is that the more complicated the matrix is, the more difficult it is to purify the actinide, and, the less sensitive the measurement.

Table 2

Measurement sensitivities for actinides in various matrices and typical sample sizes required for minimum fallout level determinations.

Elemental Concentrations		Isotopic Fingerprints
U	5×10^6 atoms	5×10^9 atoms
Pu	5×10^5 atoms	5×10^8 atoms
Am	2×10^5 atoms	2×10^8 atoms
Np	2×10^5 atoms	2×10^8 atoms

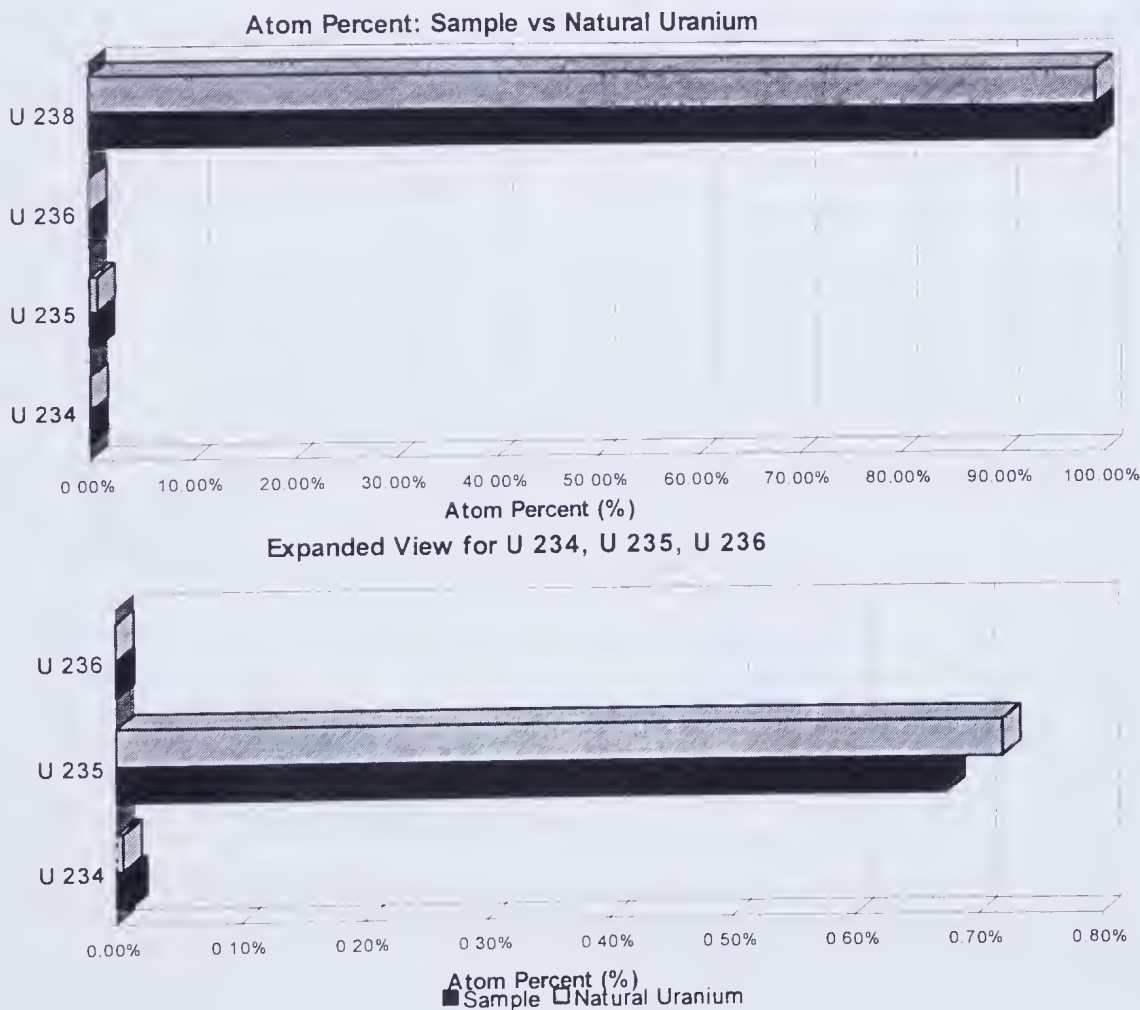
Sample Matrix	Separation Chemistry Sample Size	% Recovery
Water	2000 ml	>90
Soil	100 g	>90
Biotissue	100 g	>90

Environmental surveillance, the Pajarito Plateau

In support of the Environmental Surveillance Group at Los Alamos National Laboratory, an actinide inventory of ground waters and sediments from the surrounding Pajarito Plateau was performed. Uranium and plutonium were measured in each sample. Although anthropogenic sources were found for both U and Pu in some samples, no correlation was found between the two. One interesting fact which emerged from the study

was that no modern weapons grade plutonium was found; only pre-1960 material was found. All known sources of plutonium on the plateau were considered; pre-1960 weapons grade ($240/239 \approx 0.01$), modern weapons grade ($240/239 = 0.060 \pm 0.005$), and fallout ($240/239 = 0.18 \pm 0.02$). Only a few samples had modern 240/239 ratios, and they were shown by mixing models to be a mixture of pre-1960s and fallout. This strongly indicates that modern weapons grade material is not present in the samples submitted for analysis.

Isotope	Atom Percent	Concentration atoms/L	Concentration ng/L	Concentration pCi/L	Measurement Error(2 σ)
U 234	0.010%	1.69E+ 11	6.58E-02	4.10E-01	8.72E-03
U 235	0.675%	1.12E+ 13	4.36E+ 00	9.42E-03	2.18E-05
U 236	0.000%	4.31E+ 09	1.69E-03	1.09E-04	3.36E-05
U 238	99.315%	1.64E+ 15	6.50E+ 02	2.18E-01	5.39E-04
Total pCi/L sample:					6.38E-01
Error(±) in pCi/L:					8.74E-03
Total ng/L sample:					6.54E+ 02
Total atoms/L sample:					1.65E+ 15



- ** The U 236 concentration indicates a neutron radiation history
- ** Comparing the U 235 to natural Uranium indicates that this sample contains a depleted component
- ** The U 234 in this sample is in radioactive dis-equilibrium

Figure 1. Example of a report for uranium analysis (of groundwater); uranium isotopic and activity levels and bar graph representation of field sample in comparison with natural uranium.

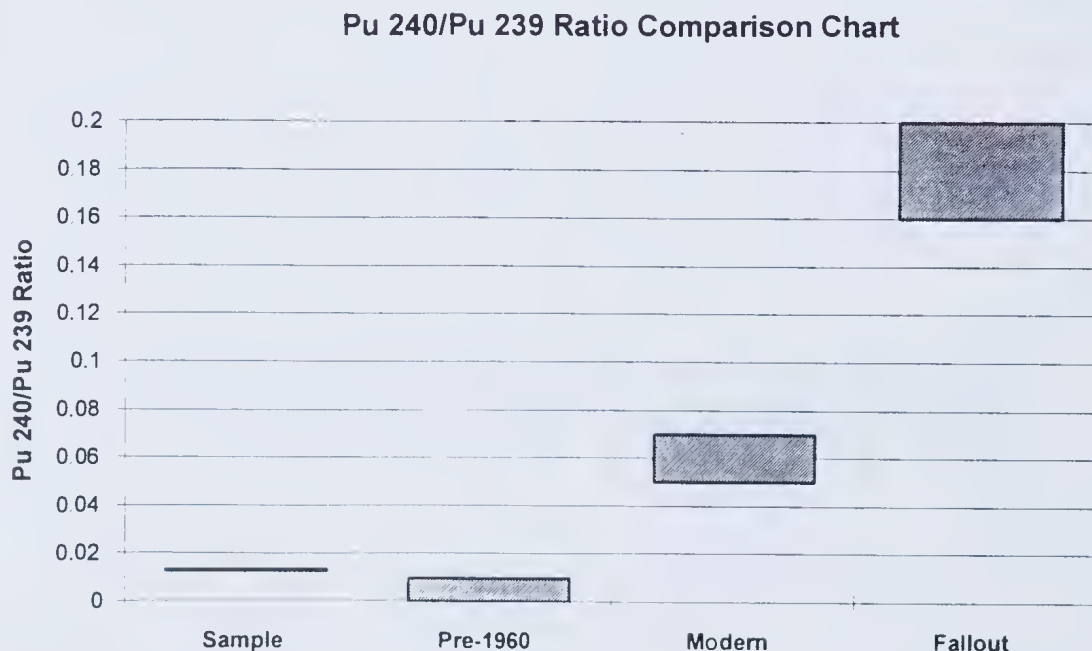
Figure 1 shows a uranium report from this study. The isotopic composition is a mixture of natural uranium, found in all samples as explained above, and depleted uranium. This sample is from groundwater, which is a good medium in which to find an anthropogenic uranium source term as soils and sediments can dilute out unnatural sources very quickly because of their high natural uranium content. A bar graph representation was chosen to compare natural uranium with the isotopic composition found in the sample, to insure that full utilization of the information by a customer with little familiarity with isotopic signatures was possible. Communications with the customer base has become a challenge in itself.

Figure 2 shows a plutonium report from this study. The bar graph shows the three known source terms for the Pajarito Plateau, old pre-1960's Pu, modern Pu, and fallout (see above for isotopic details). This sample is from ≈ 40 grams of sediment obtained from a canyon bottom. The Pu isotopic signature is clearly dominated by the old weapons grade material. This sample has a relatively high concentration of Pu but still shows the effect of mixing with fallout material.

A very accurate history of Los Alamos, at least in its earlier days, could be written from information obtained by environmental monitoring efforts. These efforts also demonstrate the ability to trace a unknown contaminant to its source term.

Isotope	Atom Percent	Concentration atoms/g	Concentration ng/g	Concentration pCi/g	Measurement Error(2 σ)
Pu 239	98.724%	2.56E+10	1.02E-02	6.32E-01	6.95E-04
Pu 240	1.273%	3.31E+08	1.32E-04	2.99E-02	3.64E-04
Pu 241	0.003%	8.82E+05	3.53E-07	3.65E-02	1.65E-02

Total pCi/g sample:	6.98E-01
Error($\pm$) in pCi/g:	1.65E-02
Total ng/g sample:	1.03E-02
Total atoms/g sample:	2.60E+10



* Note: Shaded Region Indicates Where Sample Range Must Fall for that Category

Figure 2. Example of a report for plutonium analysis (of sediment); plutonium isotopic and activity levels and 240/239 signature comparison to known source terms on the Pajarito Plateau.

IAEA 93+2 Field trial experiments

The IAEA 93+2 program was started to survey available measurement techniques which could determine compliance of signees to the NPT. The 93+2 program seeks support in;

- a) reliable analytical techniques for the determination of undeclared activities;
- b) training of staff in sampling techniques;
- c) training of staff in selected analytical techniques;
- d) search for and obtain access to environmental data bases; and
- e) to find network laboratories from member states to help relieve the heavy analytical load of the Safeguards Analytical Laboratory (SAL).

The selected techniques should be easily implemented into the IAEA structure and partially supported by member states. The first step in the process is the construction of a "clean" laboratory for the chemical preparation and measurement of environmental samples. The latter task was accomplished with the support of US funds.

The IAEA, with the support the NN-44, the US Department of Energy Office for International Safeguards, conducted a series of field trial experiments at twelve facilities around the world. The experiments were designed to demonstrate whether environmental monitoring could provide evidence of activities conducted within those facilities. These analytical techniques included; radiometric measurements, isotopic measurements by both bulk and particle, accelerator mass spectrometry, and elemental screening. Several laboratories participated, using various analytical techniques. The consensus opinion of the evaluators was that environmental monitoring could, indeed, provide useful evidence. Accordingly, the IAEA board of governors has approved the implementation of environmental monitoring as one means of strengthening safeguards. Of interest to LANL was the fact that actinides, removed from the vicinity of nuclear facilities, in any one of several matrices, could show very clearly the specific activities of that particular facility. Reactors, reprocessing plants, and enrichment plants were monitored.

One item of particular importance emerged; could our QA/QC program (Cappis *et al.* 1994) hold up to the scrutiny of the IAEA if we found evidence of a member states non-compliance with a treaty? We expressed our concern to the IAEA, which was expressing some of the same doubts. This led to confirmation that suitable performance based evaluation standards are not available, so the IAEA initiated a program to produce standards of their own. Our long history of actinide chemistry and measurement will be utilized in this program along with the participation of laboratories in at least three other countries.

Rocky flats environmental monitoring

The Rocky Flats Plant (RFP) near Denver, Colorado, built nuclear weapons components for the USDOE. While the plant was in operation, inadvertent releases of U and Pu occurred. LANL was commissioned to investigate the results of very intense remediation and containment

efforts. Retention ponds, diversion structures, and ditches were used for containment. LANL measured the U and Pu content of waters, soils and sediments over a three year period to determine the success of these efforts.

It should be noted that both inflow and outflow from a creek which passed through the plant boundaries was also monitored. The creek contained fallout Pu and natural uranium coming in to the plant, with slightly reduced concentration of U on the outflow. The outflow did, however, contain an altered isotopic signature from fallout. It should also be noted that the Pu 240/239 ratio characterized for fallout (0.169 versus 0.18), was slightly different from the world integrated average due to local inputs (Efurd *et al.* 1994; Krey *et al.* 1976).

Another observation made during this experiment was that, as expected, anthropogenic U was much more visible in surface waters than in soils or sediments. As pointed out previously, the natural U background in soil quickly dilutes out an anthropogenic source. Pu, however, was more visible in the sediments. There was approximately 50X more Pu in a gram of sediment than in one liter of water (Rokop *et al.* 1994). This is explained by the fact that Pu is adsorbed onto clay particles in the water, which settle as sediments with time. It is unclear whether the Pu is fixed into the sedimentary layers or if it can move from position to position. Experience with sampling from sedimentary clay cores suggests that it stays fixed, at least somewhat, as sedimentary layers from pre-nuclear history, before 1935, do not show Pu from fallout or any other source (Rokop, Efurd, Roensch & Poths, unpublished studies).

While the retention ponds and ditches showed the presence of Rocky Flats product, the remediation efforts were indeed very successful. The concentration of RFP actinides, with one exception, were all far below the very low standards set by the State of Colorado. The one exception, summer-time increase in Pu content of one of the retention ponds, turned out to be due to a near-by volleyball game disturbing soil previously contaminated. This water was retained and remediated until testing demonstrated the removal of Pu. No excursions above, or even close to, Colorado limits were observed outside the plant boundaries.

Conclusion

Isotopic signatures are a powerful tool that can be utilized for a wide variety of new applications. Environmental, industrial, and political spheres will be strongly influenced by their use. This tool is extremely flexible and its use is limited only by imagination.

Acknowledgements: The authors would like to dedicate this paper, and the oral presentation it follows, to Professor John de Laeter of Curtin University of Technology, for his long and distinguished career. Three words come to mind when we think of John, gentleman, eloquent, and integrity.

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Stable heavy isotopes in human health

B L Gulson

Graduate School of the Environment, Macquarie University, Sydney NSW 2109: CSIRO/EM, North Ryde, NSW 2113

Abstract

Applications of heavy stable isotopes in the field of human health are rather limited compared with applications employing radioactive isotope tracers. The elements reviewed in this paper encompass zinc, copper, iron, calcium, selenium and lead. Most research for the first five metals has addressed metabolic aspects, specifically fractional absorption ("bioavailability"). Lead isotopes, although employed for pioneering pharmacokinetic modelling research in the early 1970s, have not enjoyed widespread acceptance until more recent times. An example is given of the use of lead isotopes to detect changes to blood lead from dietary sources and the contribution of skeletal lead to blood lead.

Introduction

Most emphasis on isotopic methods in human health has been directed towards the use of light stable isotopes of carbon, nitrogen, oxygen and hydrogen for body composition, energy metabolism and macronutrient metabolism (Jones 1990). So-called "mineral" (?heavy) stable isotopes have been commonly employed as short-lived radioactive tracers. Limited use of thermal ionisation mass spectrometry (TIMS) and inductively coupled plasma mass spectrometry (ICP-MS) as well as fast atom bombardment mass spectrometry (FAB-MS) has also largely been directed towards metabolic studies, specifically bioavailability and, in the case of lead, evaluation of sources and pathways. Part of the reason for the limited use of these methods may be a narrowing of research into highly specialised fields, poor communication between disciplines, and arrogance of certain groups. Another reason for the limited use of isotopic methods in the health field is because of the perceived high cost of the measurements as a result of the high cost of the enriched isotopes. This problem is exacerbated by the use of low precision mass spectrometry (ICP-MS), which makes it necessary to use large doses of enriched isotopes.

In this paper, I will briefly review the use of stable heavy isotopes in human health, although the classification of the elements discussed may be disputed by some as not "heavy" and perhaps the term "mineral" should be employed. Elements reviewed are calcium, copper, iron, selenium and zinc with respect to; bodily functions, isotopes, methods of analysis, isotopic research and main references.

Information on bodily functions is mainly taken from Florence & Setright (1994).

Calcium (Ca)

Bodily Functions: An adult body contains ≈ 1 kg Ca, 99% of which is located in bones and teeth in the form of apatite. The other $\sim 1\%$ is found in intra- and extracellular fluids, where it plays a vital role in directing cell functions and nerve impulses. The Ca concentration in blood serum is critical and lies between narrow limits of 90-100 mg/L⁻¹. Parathyroid hormone and Vitamin D regulate Ca intake. If the intake is too low, Ca is "resorbed" from bone stores. If bone depletion continues for extended periods, this condition can give rise to osteoporosis. Maintenance of Ca homeostasis during pregnancy and lactation is critically important for females.

Isotope*	40	42	43	44	46	49
% Abundance	96.9	0.65	0.14	2.08	0.03	0.19

* Isotopes in *bold italic* are those primarily used in investigations

Methods: TIMS/ Fast Atom Bombardment-MS.

Isotopic Research: Fractional Absorption (FA) especially in the study of bone turnover status/ bone loss and osteoporosis. In metabolic investigations of bioavailability (fractional absorption, FA; the amount of the substance taken up by the body compared with the total amount introduced to the body) employing dual isotopic methods, one of the isotopes is introduced orally and the other by intravenous injection. For example, ⁴⁴Ca may be introduced orally in milk and, a short time later, the ⁴²Ca isotope is injected. Blood and urine samples are collected serially, commonly over 24 hours. For example, in a study of Chinese children on a low Ca diet of 359 mg d⁻¹, the FA was 63%; with a high Ca diet of 862 mg d⁻¹, the FA was 55% (Lee *et al.* 1994). In Caucasian children, the FA was $\approx 40\%$ (Lee *et al.* 1994). In a study of one male and one female subject, Price *et al.* (1990) measured a FA of 70%. Abrams (1993) employed TIMS to determine the rate of Ca deposition in bone and the size of the exchangeable Ca pool in bone in girls at puberty, the time of maximum growth associated with the peak of bone mass accumulation and Ca retention.

Main References: Abrams *et al.* (1991, 1993, 1994), TIMS; Eastel *et al.* (1989), TIMS; Lee *et al.* (1994), TIMS; Miller *et al.* (1989), FAB-MS; Moore *et al.* (1985), TIMS; Price *et al.* (1990), TIMS; Smith *et al.* (1985), FAB-MS; Yergey *et al.* (1987,1990,1994), TIMS.

Copper (Cu)

Bodily Functions: A 70-kg human contains about 80 mg Cu, mostly located in muscle and liver. Copper (and Fe) are the primary oxygen carriers in cells. A Fe-Cu-Zn enzyme, cytochrome oxidase, is present in mitochondria and is responsible for the catalysis of oxygen to water, an important step in cellular metabolism. Other Zn enzymes in mitochondria act as antioxidants to remove free radicals, which could otherwise promote cellular damage. Deficiency in Cu can result in anaemia, osteoporosis, reproductive failure, and heart failure.

Isotope	63	65
% Abundance	69.1	30.9

Method of analysis: TIMS.

Isotopic Research: Bioavailability (FA) for an adequate dietary intake of 1.68 mg d⁻¹, was 36%; on a low intake of 0.79 mg d⁻¹, the FA was 56%; and on a high intake of 7.5 mg d⁻¹, the FA was 12%. There is a Cu balance (homeostasis) with 0.8 mg Cu d⁻¹, and the regulation of Cu absorption and endogenous loss gives protection from Cu deficiency on the one hand, and toxicity on the other.

Main Player: Turnlund *et al.* (1989).

Iron (Fe)

Bodily Functions: In an adult male, ≈4 g Fe is distributed among the protein, haemoglobin (73%), ferritin and hemosiderin (12%), and myoglobin (14%). Haemoglobin is the main constituent of red blood cells. Its main function is to transport oxygen from the lungs in arterial blood to various organs and tissues, and return in venous blood carrying some carbon dioxide.

Isotope	54	56	57	58
% Abundance	5.8	91.7	2.14	0.28

Methods of Analysis: TIMS/ICP-MS/FAB-MS.

Isotopic Research: When added to the diet, there was a FA of ≈9% in the elderly, using faecal composites as the sampling medium (Turnlund 1983). Iron bioavailability in blood from Fe tablets was measured by Hansen *et al.* (1992). Iron distribution among the protein species transferrin, ferritin, and other haemoproteins was measured in liver and heart by Stuhne-Sekalec *et al.* (1992).

Main References: Turnlund (1983), TIMS; Stuhne-Sekalec *et al.* (1992), ICP-MS; Hansen *et al.* (1992), FAB-MS.

Lead (Pb)

Bodily Function: No natural physiological use.

Isotope	204	206	207	208
% Abundance	1.4	24.1	22.1	52.4

Methods of Analysis: TIMS/ ICP-MS.

Main References: Pharmacokinetic Modelling, Rabinowitz *et al.* (1976), Heusler-Bitschy *et al.* (1988); pregnancy/ personal monitoring, Manton (1985,1992); efficacy of chelating agents, Smith *et al.* (1994); source of Pb in humans, Yaffee *et al.* (1983), Tera *et al.* (1985), Facchetti (1989), Campbell & Delves (1989); Biokinetics of lead in pregnancy, Gulson *et al.* (1995 a,c, 1996c), Gulson & Calder (1995).

Example of the Use of Lead Isotopes: In a project on the "biokinetics of lead in human pregnancy", the primary objective was to establish if lead is released from the maternal skeleton during pregnancy and lactation (Gulson *et al.* 1995c). The main cohort were subjects from countries outside of Australia because the lead isotopic ratios in their skeleton are different from those in the "long-term" Australian population. The Australian population has ²⁰⁶Pb/²⁰⁴Pb ratios generally less than 17.0, whereas people from other countries (and especially Eastern Europe), have ratios >18.0. If a subject conceives and Eastern European lead, for example, is observed in the blood, then this is an indication that the lead is derived from maternal skeletal stores and not from Australian environmental sources such as diet, soil or dust. The subjects in this study who conceive had a matched non-pregnant control. During pregnancy, the subjects and controls were monitored monthly for blood and urine samples, and quarterly for environmental samples of house dust, drinking water, and a 6-day duplicate diet.

In one control subject, blood samples exhibited a sudden change in isotopic composition and increased lead concentration (Figure 1), in the direction which was predicted for a pregnant subject. Upon detailed questioning about dietary changes, the only plausible change was daily consumption of several glasses of beverages made with water from a newly-acquired Russian samovar. Testing of the samovar water showed it to have lead concentrations at least 20 times above fully-flushed kitchen tap water and isotope ratios consistent with Russian values.

Besides negating her role as a control, the other disconcerting aspect of these results was the rapidity of change in both isotopic composition and blood lead concentration. The implication of these rapid changes is that the bioavailability of the lead in the water is very high.

The other features of the data shown in Figure 1 are the changes in lead in blood when moving from one country to another. The blood lead concentrations in this subject are low when compared with a value of <10 µg Pb dl⁻¹, the Australian National Health and Medical Research Council National Goal for all Australians. There was little change in Pb until the samovar incident. In contrast, the isotopic composition showed a rapid decrease for all subjects from Eastern Europe when they

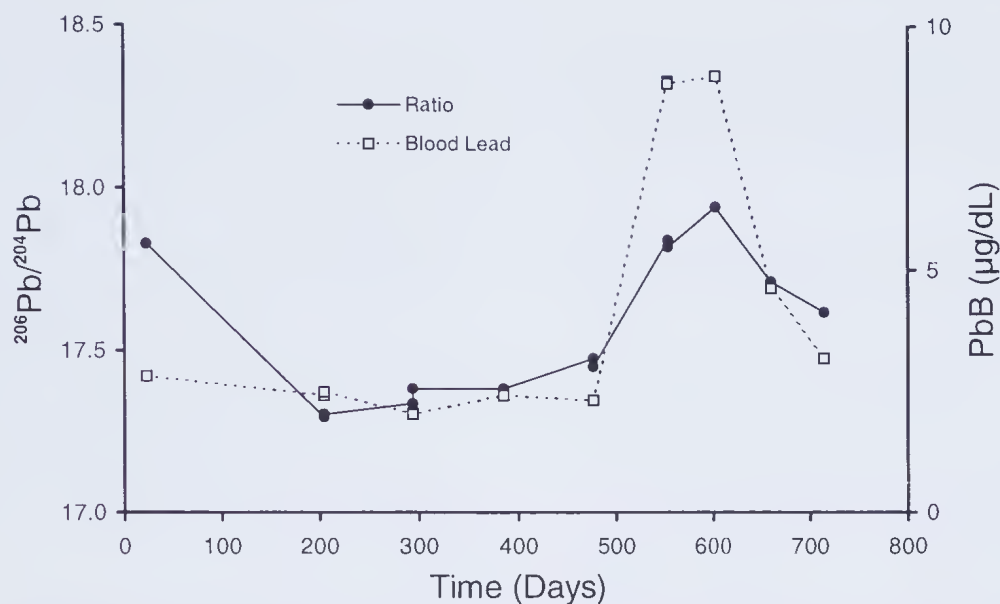


Figure 1. Time-series variation of isotope ratio, expressed as the abundance of the ^{206}Pb to ^{204}Pb , and blood lead (PbB) of a subject from Eastern Europe. The marked increase in $^{206}\text{Pb}/^{204}\text{Pb}$ ratio and PbB was traced to consumption of water from a Russian samovar.

arrive in Australia, arising from the exchange of European lead with that in the Australian environment (Gulson *et al.* 1995c). The results of this study demonstrated, for the first time, the quantitative contribution of skeletal lead to blood lead. In the case of the subject in Figure 1, skeletal lead is estimated to have a $^{206}\text{Pb}/^{204}\text{Pb}$ ratio of 18.0 and this is exchanging with Australian lead with a $^{206}\text{Pb}/^{204}\text{Pb}$ of 17.0. At 200-300 days, the $^{206}\text{Pb}/^{204}\text{Pb}$ in the blood of this subject was ≈ 17.4 , which means that approximately 40% of the lead in her blood was deriving from skeletal sources.

Selenium

Bodily Functions: Selenium is an important antioxidant. For example, glutathione peroxidase converts H_2O_2 to water, reducing cell destruction and hence combating degenerative diseases. There are 13 Se-containing proteins involved in the correct functioning of the thyroid gland. Selenium is also a strong inhibitor of platelet aggregation, a process involved in strokes, heart disease and cancer metastases.

Isotope	74	76	77	78	80	82
% Abundance	0.9	9.0	7.5	23.5	50	9.0

Methods of Analysis: ICP-MS.

Isotopic Research: FA is up to 70% when present as selenomethionine (organic form in food) compared with 40% in inorganic form. Selenium acts synergistically with Vitamin C as an antioxidant.

Main References: Kasper *et al.* (1984), Martin *et al.* (1988, 1989a,b), Sirichakwal *et al.* (1985), Solomons *et al.* (1986).

Zinc

Bodily Functions: In an adult, there is $\approx 2\text{g}$ Zn in muscle, bone and tissues. It is essential for bone formation, wound healing, immune system function, ageing, sexual

function, anorexia nervosa, and reduction of cadmium toxicity. Over 200 enzyme systems require Zn for structural integrity or catalysis, including synthesis of DNA and RNA.

Isotope	64	66	67	68	70
% Abundance	48.8	27.8	4.1	18.6	0.62

Methods of Analysis: TIMS/ICP-MS/FAB-MS.

Isotopic Research: A study by August *et al.* (1999) indicated that for a diet with Cu addition, FA was $\approx 40\%$ in the young and $\approx 21\%$ in the elderly; for a diet with no addition of Cu, FA was $\approx 31\%$ in the young and $\approx 17\%$ in the elderly (Turnlund *et al.* 1986). Later work, however, by Couzy *et al.* (1993) using radioisotope methods indicated that age differences were not significant for Zn FA. In another study, Fairweather-Tait *et al.* (1992) showed that there was no difference in the FA ($\approx 30\%$) of Zn for white compared with wholemeal bread. Jackson *et al.* (1984) and Lowe *et al.* (1993) investigated Zn biokinetic modelling (definition of Zn compartments in the body).

Main Players: Turnlund *et al.* (1984, 1986, 1991), TIMS; Jackson *et al.* (1984), TIMS; Couzy *et al.* (1993), radioisotopes; Knudsen *et al.* (1995), ICP-MS; Eagles *et al.* (1989); Janghorbani *et al.* (1984, 1990), ICP-MS.

Concluding comments

This brief review illustrates that there is considerable scope for investigations in human health using isotopic techniques with stable isotopes. One concern that I have is whether or not many of the metabolic experiments for bioavailability are really applicable to "real life". The elements are commonly introduced as pure compounds and these species may not be in the appropriate bioavailable form. For example, the FA of Fe was measured in one experiment as $\approx 9\%$ in elderly subjects. It is fairly well established that the bioavailability of Haeme

Fe varies according to the food item: in meat it is $\approx 20\%$, in fish $\approx 6\%$, in cereals and vegetables $\approx 2-5\%$, and in breast milk the bioavailability is $\approx 50\%$ versus $<5\%$ for formula. Furthermore, drinking alcohol with meals enhances bioavailability of Fe (Florence & Setright, 1994).

Acknowledgements: The Biokinetics of Lead in Human Pregnancy study is largely financed by a US National Institute of Environmental Health Sciences Grant NO1-ES-05292. The research at Broken Hill was partly supported by the NSW Environment Protection Authority.

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Lead isotopes and pollution history

K J R Rosman & W Chisholm

Department of Applied Physics, Curtin University of Technology, Bentley, WA 6102

Abstract

Lead is one of the seven metals of antiquity and its production is highly correlated with the development of industrial civilisations. This paper reviews the awakening during the 1960s of modern humans to the environmental and health problems associated with the use of lead. The difficulty of measuring lead received little attention until the mid 1960s when it was realised by geochemist C C Patterson and colleagues at the California Institute of Technology that the world was immersed in a lead mist. This awareness prompted analysts to develop clean-air laboratories and to take special precautions when collecting and analysing samples for lead. Thermal ionisation mass spectrometry has played a vitally important role in this process by offering a high-sensitivity detection tool, and the means of uniquely identifying artifact lead contamination through its isotopes. Today this tool is being used to identify the origin of lead in natural archives such as the Greenland and Antarctic ice sheets. This paper discusses the development of this field.

Introduction

Significant lead production began about 5000 years ago with the discovery of cupellation. Lead sulphide ores were smelted to produce lead-silver alloy which yielded metallic silver on oxidation. Smelting led to local pollution but also released lead to the atmosphere. However it was only during Greek and Roman times, about 2500 years ago, that atmospheric pollution from this source reached levels where evidence of the fossil remnants could be detected in Greenland ice (Hong *et al.* 1994).

Lead has been associated with human health problems since antiquity and may have contributed to the fall of Rome (Nriagu 1983). Its toxic effects on humans are now well understood and childhood lead poisoning is of great concern (Mushak *et al.* 1989; McMichael *et al.* 1988). Lead is a non-degradable poison and has been produced at an increasing rate during the twentieth century. Vast quantities have been used in paint and as an anti-knock agent in petrol, creating a problem of global dimensions which this and future generations must resolve (Rabin 1989; Nriagu 1990; Needleman 1991).

Although lead has created tremendous problems for mankind, the formation of its isotopes by radioactive decay allowed the first accurate determination of the Earth's age (Patterson 1956). The array of isotopic abundances found in crustal rock and lead ore has been the key to the identification of anthropogenic lead in ancient ice and is the basis of a method for tracing lead and associated pollution around the globe. The two primary instruments used for these studies are the mass spectrometer and the ultra-clean sample preparation laboratory. The last three decades have witnessed dramatic improvements in mass spectrometer sensitivity ($>10^6$ for some elements) through the development of new ionisation methods (Cameron *et al.* 1969; Rosman *et al.*

1984) and vastly improved techniques for sampling and preparing small samples for analysis (Patterson & Settle 1976). These techniques have now been refined to the point where the isotopic composition of lead in remote snow and ice can be reliably measured (Rosman *et al.* 1993).

This paper briefly reviews the motivation for constructing a lead pollution history for the global atmosphere and shows how the measurement of lead isotope abundances complements concentration measurements by providing a method to identify the source of pollution.

Pollution History

A variety of natural archives have been used to construct pollution histories; these include river, lake and marine sediments, peat bogs, glaciers, the polar ice caps and tree rings. In these archives, the anthropogenic species are trapped in layers and remain essentially isolated from each other. A pollution history can be established by measuring the species and the corresponding deposition age. Time scales for these archives vary from years to millennia.

The impetus for constructing a pollution history of lead for the Northern Hemisphere came from Clair C. Patterson of the California Institute of Technology (CIT), who, together with colleagues T Chow and M Tatsumoto, found that industrial lead was having a profound influence on the lead content of the oceans and atmosphere. Although the measurements of lead in sea water in their earlier studies were later found to be in error by a large amount due to contamination problems, their conclusions were correct. Following the publication of a paper entitled *Contaminated and Natural Environments of Man* (Patterson 1965), Patterson directed his research effort towards understanding the impact that anthropogenic lead was having on the biogeochemical cycle of lead. This paper created much public interest, controversy amongst scientists, and corporate concern. Differences of opinion

between scientists often arose from a lack of awareness of the real difficulties of analysing lead at low concentration, either in the field or in the laboratory. Ignorance of these problems still persists today.

Patterson began his 1965 paper: "A prevailing belief is that industrial and natural sources contribute more or less equal amounts of lead to the body burdens of the general population.". He proceeded to demonstrate with geochemical arguments, using the relatively poor data of the time, that the average resident of the U.S.A. had a body burden for lead one hundred times above natural levels. Questions raised in his paper were the subject of CIT research for the following three decades. One recommendation arising from his study was the need to establish "natural" lead levels as opposed to the "typical" levels found in modern environments, and so a lead pollution history for the Northern Hemisphere extending back in time almost three millennia was constructed.

The concentration of lead was measured in dated layers of Greenland snow and ice extending from 1965 AD back to 800 BC (Murozumi *et al.* 1969). This was a remarkable accomplishment for its time. The time series covering the period 1753-1965 was established by analysing preserved layers of snow and ice taken from the walls of trenches and shafts at Camp Century (77°10'N, 61°08'W, elevation 1.87 km) and a site 80 km away in north west Greenland. The ice sample dated 800 BC was collected from Camp Tuto (76°25'N, 68°20'W). These measurements initially caused controversy among geochemists because they raised doubts about the quality of published data on polar snow, but the results were eventually confirmed and extended (Ng & Patterson, 1981; Boutron *et al.* 1991; Candelone *et al.* 1995). Figure 1 summarises the results of these measurements.

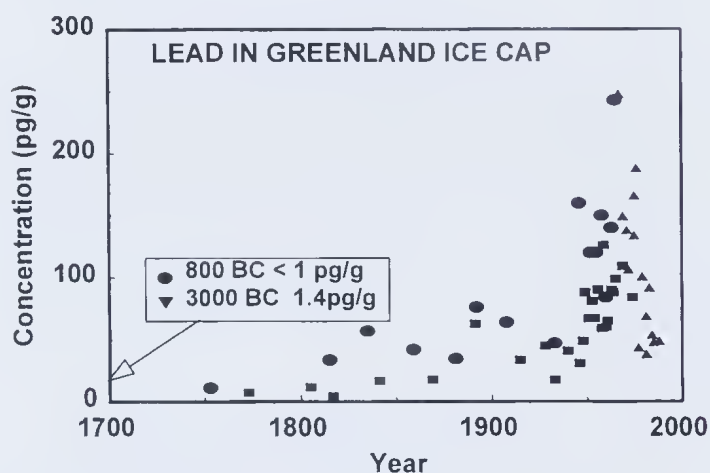


Figure 1. Changes in the concentration of lead in Greenland snow and ice dating from 3000 BC to the present. Adapted from Murozumi *et al.* (1965) - ellipses; Boutron *et al.* (1991) - triangles; Candelone *et al.* 1995 - squares, Ng & Patterson 1981 - inverted triangle.

To identify the source of lead emissions to the atmosphere, it is necessary to tag each source in some way. Isotopic fingerprinting can be very effectively used for lead when there are natural variations between sources. Early workers were well aware of the potential of this technique and were successful in identifying sources of

local pollution (Chow & Johnstone 1965), but only recently has it been possible to use the technique to investigate sources of atmospheric pollution on a hemispheric scale (Rosman *et al.* 1993).

Lead Isotopes

Lead has four naturally occurring stable isotopes, ^{204}Pb which was only formed by nucleosynthesis and three others which are also end products of radioactive decay chains: $^{238}\text{U} \Rightarrow ^{206}\text{Pb}$, $^{235}\text{U} \Rightarrow ^{207}\text{Pb}$ and $^{230}\text{Th} \Rightarrow ^{208}\text{Pb}$ with half-lives 4.5×10^9 , 0.71×10^9 and 14×10^4 years respectively. Consequently, lead isotopes in rocks and minerals of different chemical composition and in lead ore bodies of different ages, which are the source of industrial lead, display large abundance variations that can easily be measured in a mass spectrometer.

Soddy, who introduced the term "isotope", suggested in 1913 that because lead was formed by the radioactive decay of uranium and thorium, then minerals rich in these elements would have lower and higher atomic weights, respectively, than common lead. This prediction was confirmed within a year by number of reports (Table 1) and provided early confirmation of the existence of isotopes.

Table 1

Early evidence of natural variations in the abundance of lead isotopes (from Aston 1942). Minerals: ^aCeylon thorite, ^bCarnotite, ^cNorwegian cleveite, ^dNorwegian thorite.

Investigators	atomic weight		
	high U	common Pb	high Th
	≈207.19		
Soddy & Hyman (1914)			207.694 ^a
Curie (1914)	206.36 ^b		
Richards & Lemberg (1914)	206.08 ^c		

Lead Isotopes in the Environment

Interest in the use of isotope abundance variations for tracing sources of industrial lead began in the early 1960s (Tatsumoto & Patterson 1963; Chow & Johnstone 1965) and evolved from earlier geochemical studies by Chow, Patterson and Tatsumoto who had all been associated with the same CIT laboratory. Since this time, lead isotopes have been used as natural tracers on a number of occasions, but the number of studies have been relatively few considering the potential of this approach for solving environmental problems. One particularly significant early study was that by Chow *et al.* (1975) who assessed lead isotopic abundance variations in aerosols, gasoline and soil in various countries by spot sampling during the period 1964 - 1974. They also monitored temporal variation in San Diego (USA) aerosols over the same period which revealed a clear trend in isotopic composition.

Since this time, pollution histories that include isotopic data have been published for a range of different natural archives, including for example river sediments (Shirahata *et al.* 1980), lake sediments (Ritsen *et al.* 1994) marine sediments (Hirao *et al.* 1986), coral (Shen & Boyle 1987) and snow (Rosman *et al.* 1993).

Isotopic Fingerprinting in Snow and Ice

Pollution histories based on lead in recent snow and ice are relatively simple to interpret because the natural background contribution is generally negligible. Murozumi *et al.* (1969) showed that the background (pre-Roman) concentration of lead in remote Greenland snow and ice was only $\approx 1 \text{ pg g}^{-1}$, which was cleaner than the water found in most analytical chemistry laboratories.

Reliable isotope abundance measurements of lead in pre-industrial ice demand that the following be available:

1. ultra-clean procedures for the acquisition and storage of field samples;
2. ultra-clean decontamination procedures;
3. ultra-clean sample storage;
4. ultra-clean sample processing for mass spectrometry;
5. sensitive high precision mass spectrometry.

Murozumi *et al.* (1969) showed incredible skill in measuring pg g^{-1} concentrations, of lead in Greenland ice. To minimise the contributions from artifact contamination they collected 19 kg or 50 kg size blocks of ice. Thirteen years later, Ng & Patterson (1981) required only 100-200 g samples to confirm the results of the earlier study. The corresponding laboratory blanks for these two studies were $\approx 100 \text{ ng}$ and 160 pg , the later amounting to $\approx 30\%$ of the cleanest sample analysed.

The size of samples typically used today for isotopic analyses vary from 1-50 g depending on their lead concentration, while the total laboratory processing blank has improved steadily to $\approx 3 \text{ pg}$ in 1993 (Rosman *et al.* 1993) and finally $\approx 0.5 \text{ pg}$ today (author's laboratory). The improvement in the blank/sample ratio in the 1990s arose from the realisation that snow collected at remote locations is relatively free of impurities and consequently processing can be kept to a minimum, and should ideally be avoided. Whereas earlier studies (Murozumi *et al.* 1969; Ng and Patterson 1981; Boutron & Patterson 1986) using mass spectrometers for lead concentration measurements attempted to purify the lead using chemical methods such as ion exchange or solvent extraction, current practice is to concentrate the sample by evaporation in an ultraclean environment (Rosman *et al.* 1993, 1994a,b; Chisholm *et al.* 1995).

The capability of current methods can best be illustrated with measurements on the purest laboratory water. Figure 2 shows measurements of lead in three different masses. The concentration of lead in the water is calculated from the gradient of the line through the points (0.013 pg g^{-1}), and the procedural blank is determined from the intercept (0.47 pg). In practice, ice samples are normally measured only once or twice, procedural blanks are checked by monitoring critical reagents, and the effectiveness of the beaker cleaning procedures and the quality of the laboratory water are checked by evaporating equivalent volumes of ultra-pure water in beakers prior to using them for a sample.

Lead concentrations are measured by isotope dilution mass spectrometry (IDMS) with a minor variation. A known amount of ^{205}Pb -enriched tracer (half-life 1.5×10^7) is mixed with the sample prior to analysis. The quantity

LABORATORY WATER

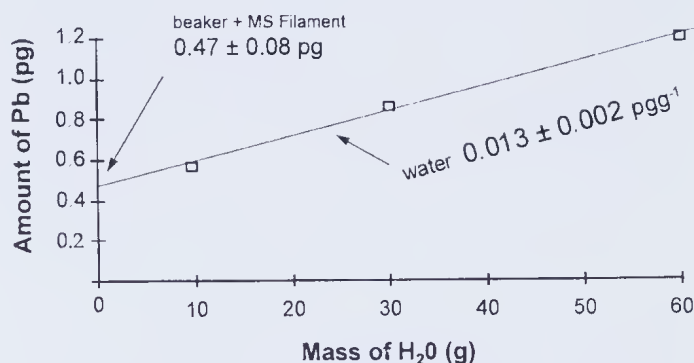


Figure 2. The concentration of lead in ultra-pure laboratory water. The gradient of the line yields the lead concentration and the intercept gives the analytical blank.

of natural lead can be determined from the measurement of the mixed lead mass spectrum. Because ^{205}Pb does not occur naturally, the use of this tracer permits the isotopic composition to be determined in the same measurement.

A vital step in the chain of procedures needed for a reliable measurement of lead in ice is the decontamination process. The purpose is to mechanically remove contaminated ice, layer by layer, ideally resulting in a central core of uncontaminated ice. Each layer is analysed to confirm the effectiveness of the procedure. (Ng & Patterson 1981; Candelone *et al.* 1994). Figure 3 shows the concentration profile for a section of the Vostok ice core drilled in Antarctica by a team from the former Soviet Union (Chisholm *et al.* 1995). In this case, however, the contaminant lead penetrated the central core and only an upper limit of concentration could be given. The criterion for an uncontaminated central core is that the concentration must reach a constant value. This approach was developed by Ng & Patterson (1981) and is still the most reliable method of validating the purity of the central sample. However the advent of isotope abundance measurements added another dimension to

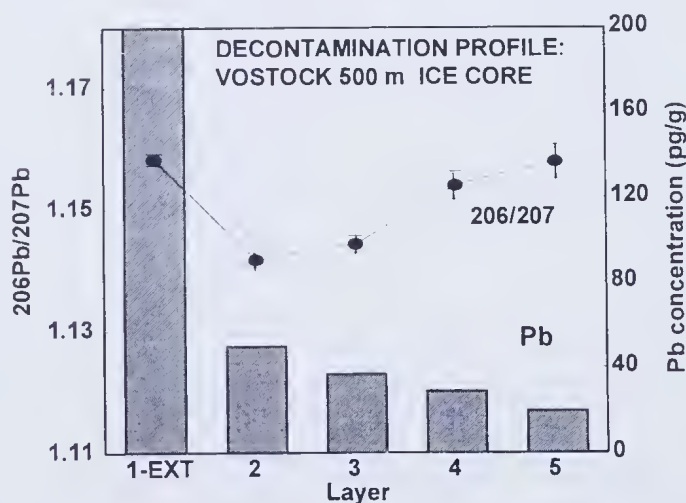


Figure 3. Lead concentration and isotopic ratio profile across a Vostok ice core. The sample was taken from a depth of 500 m (26.2 ka BP) using a thermally drilled hole with kerosene as the retaining fluid.

this process by allowing different sources of contamination to be resolved. In Figure 3, the outer layers show an initial decrease in isotopic ratio then an increase, but never reach a constant value. This pattern suggests that there are two sources of artifact lead in addition to the natural component. The lead concentration is highest on the outside and also continues to change as the centre of the core is approached, confirming that artifact lead is still present. This analysis can only yield an upper limit of concentration and a lower limit of isotopic ratio.

Lead Pollution History of the Northern Hemisphere

The Greenland ice cap penetrates the troposphere and rises to an altitude of ~ 3.23 km at Summit (72°35'N, 37°38'W) near the centre of the island. Aerosols are scavenged by falling snow which accumulates on the ice cap and is eventually converted to ice when it reaches a depth of about 80 m. The analysis of snow and ice from various depths provides a record of the pollution history of the Northern Hemisphere. The analysis of pre-Roman ice is essential for a correct interpretation of post-industrial changes while much older ice provides useful information on early climatic conditions.

The oldest ice collected to date (~250 ka) was retrieved recently by the European GRIP (Greenland Ice Core Program) and the United States GISP (Greenland Ice Sheet Program) teams who drilled ~3 km to the basement at two sites near Summit (Dansgaard *et al.* 1993; Grootes *et al.* 1993). Shallower sampling in the same area has also provided interesting complementary information. For instance, an 11 m snow core taken with a polycarbonate hand-operated auger (to minimise contamination) and a 70 m electromechanically drilled core were both taken during the recent European "Eurocore" program (Boutron *et al.* 1991; Candelone *et al.* 1995). Boyle *et al.* (1995) also report lead concentration measurements to a depth of 6 m at Summit. In the latter study, two series of samples were taken - one from the walls of a snow pit and the other with a solar powered electric coring rig.

The analyses of these samples has allowed a lead pollution history of the Northern Hemisphere to be

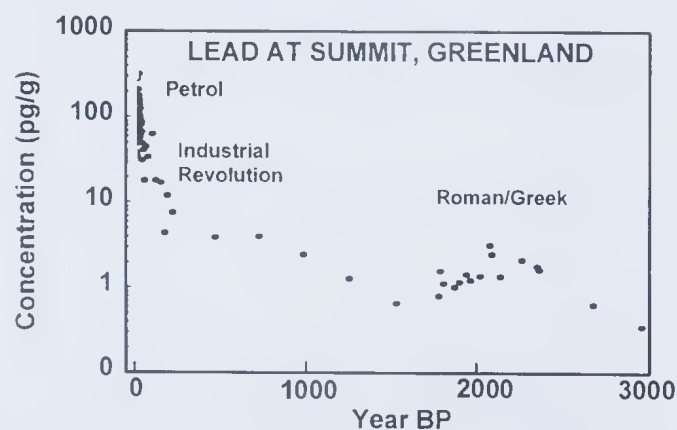


Figure 4. Recent measurements of the lead concentration in Greenland ice extending back to 3000 BP. Events causing significant changes in lead emissions to the atmosphere are identified, namely the introduction of leaded petrol, the Industrial Revolution, and the Greek/ Roman civilisations. Data from Boutron *et al.* (1991), Candelone *et al.* (1995) and Hong *et al.* (1995).

constructed covering one full glacial cycle (Boutron *et al.* 1991; Candelone *et al.* 1995; Hong *et al.* 1994), and has confirmed the earlier measurements by Murozumi *et al.* (1969). Figure 4 summarises the results of these measurements and shows the periods of history when lead pollution was prominent.

Only during the 1990s have reliable lead isotope abundance data in Greenland and Antarctic snow and ice become available. When Boutron *et al.* (1991) analysed an 11 m snow core from Summit they attributed the decreasing concentration of Pb during the 1980s to the rapid reduction in the use of leaded gasoline in the United States. The analyses of lead isotopes in these samples by Rosman *et al.* (1993, 1994a) confirmed this hypothesis. The variation of the $^{206}\text{Pb}/^{207}\text{Pb}$ isotope ratio found in these samples is shown in Figure 5 with the signatures of lead used in United States and Eurasian gasoline superimposed. From these data, Rosman *et al.* (1994a,b) computed the concentrations of US and Eurasian lead in Greenland snow (Figure 6). The results were in excellent agreement with the known pattern of leaded petrol consumption.

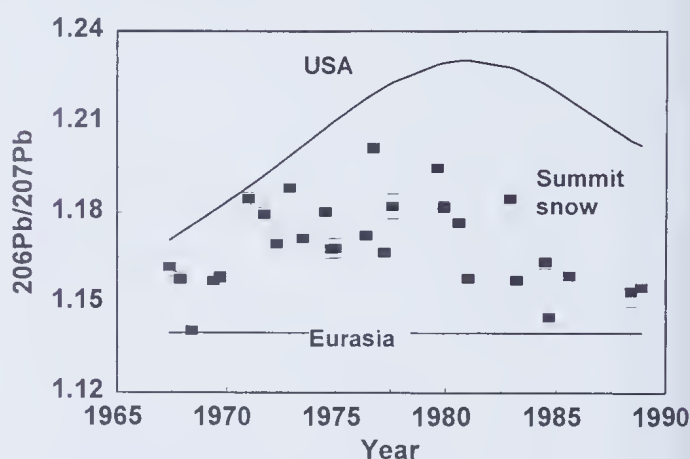


Figure 5. The $^{206}\text{Pb}/^{207}\text{Pb}$ isotopic ratios in snow from Summit, central Greenland (Rosman *et al.* 1993). The USA and Eurasian isotopic signatures taken from the literature are shown (Adapted from Rosman *et al.* 1994a).

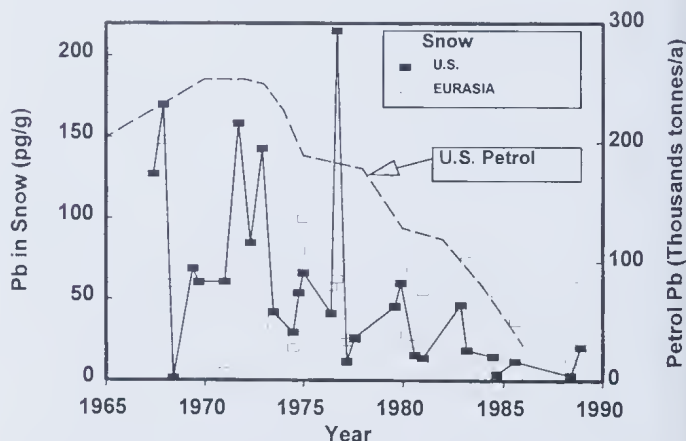


Figure 6. Comparison of USA and Eurasian lead in Summit snow with lead emissions from USA petrol. The concentrations were calculated from the isotopic ratios shown in Figure 5 and the total concentration of lead in the snow (Adapted from Rosman *et al.* 1994a).

Hong *et al.* (1994) reported relatively high lead concentrations in two thousand year old ice from the GRIP ice core and attributed this to pollution of the atmosphere by industrial emissions caused by the Greek and Roman civilisations. Preliminary measurements on these samples now show a significant decrease in the $^{206}\text{Pb}/^{207}\text{Pb}$ ratio which correlates with the enhanced lead concentration. These isotopic measurements are highly significant because they provide definitive evidence that this lead had an anthropogenic origin (Rosman *et al.*, 1995).

Lead Pollution History of the Southern Hemisphere

The Antarctic ice sheet is ideally located to record pollution in the Southern Hemisphere but the transfer of pollutants to Antarctica from populated regions is less direct than it is for Greenland. Although both land-masses extend to $\approx 60^\circ$ latitude, Greenland is flanked by continents which extend into the Arctic whereas Antarctica is isolated from the influence of other land masses by the circumpolar convergence, which is a extremely effective barrier. Even so, Antarctica is highly polluted with anthropogenic lead although the concentrations in surface snow are one to two orders of magnitude lower than in Greenland.

Because the concentrations are very low, few reliable lead data for Antarctic snow and ice are available. Using elaborate sample collection and decontamination procedures, Boutron & Patterson (1987) measured concentrations as low as 2.3 pg g^{-1} in snow 433 km from the coast near the French base of Dumont d'Urville. This snow fell near the end of 1982 and during 1983. Geochemical arguments were used to show that $\approx 80\%$ of this lead was anthropogenic. Recent isotopic abundance measurements on the same sample gave a $^{206}\text{Pb}/^{207}\text{Pb}$ ratio of 1.16 compared with 1.07 for petrol and 1.25 for natural dust which indicated that at least 50% of the lead was anthropogenic (Rosman *et al.* 1994b).

Lead histories for Antarctica are limited to a few reliable studies. Even so, only selected reports will be identified here. Recently Wolff & Suttie (1994) produced a time series from the 1920s and observed concentrations of $\approx 2.5 \text{ pg g}^{-1}$ for 1920-1960 increasing to a peak between 1978-1980 of $\approx 10 \text{ pg g}^{-1}$ then falling back to $\approx 5 \text{ pg g}^{-1}$ by the mid 1980s. Boutron & Patterson (1986, 1987) reported time series for ancient ice which they obtained from a thermally drilled core from Dome C ($77^\circ 39'\text{S}$, $124^\circ 10'\text{E}$ and elevation 3.24 km; samples to 27 ka BP) and an electromechanically drilled core from Vostok ($78^\circ 28'\text{S}$, $106^\circ 48'\text{E}$ and elevation 3.49 km; samples to 155 ka BP). Concentrations at Dome C were as low as 0.3 pg g^{-1} during the Holocene (back to 13 ka BP) but they peaked at 29 pg g^{-1} during the coldest period of the last ice age (≈ 21 ka BP). Corresponding concentrations for the earlier glacial cycle at Vostok were 2.4 pg g^{-1} and 19.8 pg g^{-1} respectively.

Only three measurements of lead isotopes in ancient Antarctic ice have been reported. These include two Dome C ice core samples dated at 7.5 ka BP and 14 ka BP, which gave $^{206}\text{Pb}/^{207}\text{Pb}$ ratios of 1.25 and 1.20 respectively (Rosman *et al.* 1994b; Chisholm *et al.* 1995).

The Future of Lead Isotopes and Pollution History

Lead isotopes offer a powerful tool for identifying sources of pollution and they are a valuable complement to concentration measurements.

Measurements on recent Greenland snow have already demonstrated how leaded petrol emissions from the USA and Eurasia can be identified and their relative contributions assessed. Work is currently in progress that will extend the lead isotope record for the Northern Hemisphere back to Roman times and beyond. These data will provide new and interesting information regarding the source of the lead emissions in earlier times.

Measurements on deep cores both from Greenland and Antarctica will also provide additional information on the climatic conditions which existed on Earth during the recent glacial cycles. The concentration of the lead in the ice and its isotopic composition will reflect the atmospheric conditions and the geographical origin of the dust containing the lead.

Very few isotope abundance measurements have been made in Antarctica but the technology is now available for the measurements of existing cores to proceed. Detailed measurements at high depth resolution will be needed to identify seasonal influences and to follow the development of industry in the Southern Hemisphere. It is anticipated that high resolution cores (high deposition rates) drilled in the Law Dome by Australian teams will provide samples suitable for such studies.

The origin of the dust reaching Antarctica is not known at present. Evidence from isotopic (Grousset *et al.* 1992; Rosman *et al.* 1994) and geochemical (Delmas & Petit 1994) studies are in agreement but conflict with predictions from global circulation models (Joussame 1993). Isotopic studies on snow and ice coupled with atmospheric monitoring of present day aerosols will help to resolve this problem.

The skills required for the collection, decontamination, elemental and isotopic analysis of the cleanest snow and ice samples are not limited to one laboratory. This is an activity which continues to benefit greatly by international scientific collaboration.

Acknowledgements: We are indebted to John De Laeter who established the Curtin laboratory in the late 1960s and enthusiastically promoted the application of mass spectrometry to environmental science. The Australian Research Council has supported Curtin research on lead isotopes in snow and ice cores described in this paper. This later work is the result of a very successful collaboration with Claude Boutron of the Laboratory for Glaciology and Geophysics of the Environment, Grenoble, France.

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Surface ionization sources and applications

J E Delmore, A D Appelhans, J E Olson, T Huett, G S Groenewold, J C Ingram
& D A Dahl

Idaho National Engineering Laboratory, Box 1625, Idaho Falls, Idaho USA 83415-2208

Abstract

A series of new instruments have been developed for the study of ion emission from hot inorganic deposits, these being; a tube ion source, an ion source imaging instrument, and an ion/neutral mass spectrometer. Techniques have been developed for applying these instruments to the development of new ion emitters as well as in studying the properties of previously developed emitters. This line of study has led to a new type of anion emitter that has found use as the primary gun for the static SIMS analysis of insulators. Applications of the new primary anion gun to the measurement of environmental contaminants are discussed.

Introduction

Surface ionization (SI) was recognized at least 70 years ago as a scientific phenomenon, and has been employed as an analytical tool for almost 60 years. SI has been investigated in a variety of contexts, but in general this is an area that has been understudied, in spite of the wide spread applications in mass spectrometry for the measurement of isotope ratios. Of the studies that have been conducted on the fundamentals of SI, most have involved the study of atoms striking a pure, hot metal surface. Few have investigated mechanisms of the sublimation of ions from complex deposits. We have been interested for many years in the chemistry of deposits that directly sublime (or evaporate in the case of liquid deposits) ions from the surface. This is a complex field, and after many years we are evolving a series of tools which are helping us to better understand the inorganic and physical chemistry which determines which types of emitters, when heated, will efficiently produce ions. This is not a mature field, however, and could easily accommodate additional investigators.

In the early 1960s the Idaho National Engineering Laboratory (INEL) began a program for the measurement of fission yields for the major fissioning species in a variety of types of nuclear reactors. This led development of methods for performing isotope ratio measurements on a wide range of fission product elements. The culmination of these studies were the Oklo Natural Fission Reactor studies were performed jointly between Los Alamos National Laboratory, Curtin University and the INEL (Loss *et al.* 1988; Curtis *et al.* 1989; Loss *et al.* 1989). The development of new methods for measuring isotope ratios led to an interest in the chemistry of the deposits on the hot filaments which emitted ions. These activities have in turn been developed into a new line of ion guns for use as the primary ion beam in static secondary ion mass spectrometry (static SIMS) for the measurement of environmental pollutants.

If one studies a variety of ion emitters, over time there will be certain systems which produce ions with unexpectedly high intensity ("boomers"). Examples of this type include (but are certainly not limited to);

- 1) the alkali metal cations from aluminosilicates (typically, but not always, zeolites) (Beck *et al.* 1989; Satoh *et al.* 1987; Pargellis & Seidl 1978);
- 2) borate (BO_2^-) from rare earth oxides;
- 3) perrhenate (ReO_4^-) from barium perrhenate in europium and ytterbium oxide matrices (Delmore *et al.* 1995);
- 4) halides (Cl^- , Br^- , I^-) from lanthanum hexaboride (Rachidi *et al.* 1976; Delmore 1982).

When one attempts to intentionally produce an emitter which produces ions as efficiently as those which are produced from contaminants, the results can sometimes be disappointing. An example is iodine from lanthanum hexaboride (LaB_6). Iodine present as a contaminant in LaB_6 is ionized with much higher efficiency than any intentionally added for analysis, and similar issues arise with all of the above examples. These are examples of the importance of the chemical form of the element or molecule to be ionized; ionization efficiency can drop dramatically unless the appropriate chemical species is identified and added in that form.

We have chosen to investigate these high intensity "boomers" because they are easier to study, and hence we would be more likely to discover basic features that would lead to fundamental understandings. The two emitters which we have studied the most are alkali metal zeolites and perrhenate/rare earth oxides, and both appear to be "scalable." That is, the intensity of the emitted ions can be increased by increasing the size of the deposit, by increasing the loading of the species to be ionized in the matrix, and by increasing the temperature. This is in contrast to the molten glass ion emitters (silica gel type matrices) which are much more difficult (perhaps impossible) to scale (Huett *et al.* 1995).

There will be three main themes developed in this paper. First, we will concentrate on the two ion emitters that have found use in this laboratory, alkali metal cat-

ions from zeolite, and perrhenate (ReO_4^-) anions from a europium oxide/barium perrhenate ceramic emitter. Second, we will briefly describe two instruments built specifically for the study of these emitters, and methods developed to study these emitters. Third, we describe how these two ion emitters have been incorporated into ion guns used for SIMS instruments, and show that the ReO_4^- anion gun has proven to have great utility for the SIMS analysis of partial monolayers of adsorbates on insulating surfaces.

Experimental procedures

The literature has many references to the emission of alkali metal cations from aluminosilicates, and in practice almost any zeolite will upon heating emit large currents of alkali metal cations. These zeolites can be soaked in aqueous solutions of an alkali metal chloride or nitrate at room temperature and when the material is heated to 700 to 800°C (Beck *et al.* 1989) in vacuum, will emit that particular alkali metal cation. These emitters (for all of the alkali metals) are widely used in ion guns for a variety of applications, and are even sold commercially by several companies.

The perrhenate anion emitter was developed at the INEL and has been used as the active element in several ion guns used for static SIMS. These SIMS instruments have been used for a wide range of analyses, which have opened many new analytical possibilities. The perrhenate anion emitter is a ceramic material, the composition of which is being published elsewhere (Delmore *et al.* 1995), and operates in the range of 800 to 900°C. It can deliver up to 10 nA into a 2mm spot size, but typically is operated at about 100 pA.

Hardware called the "tube ion source" has been used in most of our studies. It entails pressing the powdered emitter material into a tube, spot welding this tube to rhenium ribbons, and then spot welding the ribbons to the posts of a filament support (Delmore *et al.* 1994). The zeolite-based materials were pressed into 304 stainless steel tubes which were pinched off at the back. The perrhenate emitters were pressed into rhenium tubes with a tantalum plug in the back.

Two instruments have been developed for testing the properties of these emitters. These have proven to be very useful in helping to understand the ion formation mechanisms. These instruments are an ion source imaging instrument (Delmore *et al.* 1994) and an ion/neutral mass spectrometer. The ion source imaging instrument utilizes a tube ion source mounted in an imaging lens, and the emitted ions are projected onto a screen where the image can be recorded.

The ion/neutral mass spectrometer is still very early in the development cycle. It employs a source which combines both a surface ionization capability and an electron impact capability for ionizing the neutral gases which are desorbed from the emitter material. A computer system, which is now working for most of the desired functions, is being developed to control the mass scanning, the data collection, correlation and display, and ion source focusing. The focusing voltages for the two ionization modes are very different, and the computer program can step between these modes, so that a

clear definition can be made between ions originating from the two ionization modes. The value of this instrument is that it allows both the ion and the neutral components to be individually mass-analyzed so that the relative proportions of ions to neutral components, and the change in the ratio of these components with time, can be measured. This in turn gives insights into ion formation mechanisms, and permits optimization of the emitter being studied. An attempt to quantify the ratios of ions to neutrals has not yet been made.

The perrhenate anion emitter has been incorporated into an ion gun, which in turn has proven to be very useful in static SIMS instruments used for the analysis of insulating materials. There are five static SIMS instruments in our laboratory which use this type of ion gun, two using single quadrupoles (SQSIMS), one using a triple quadrupole (TQSIMS), and two using ion traps (ITSIMS). The SQSIMS have been described elsewhere (Appelhans *et al.* 1987; Appelhans & Delmore 1989; Appelhans *et al.* 1990; Appelhans *et al.* 1994).

Results

Ion Emitters

The ion source imaging instrument has been used quite extensively to image three types of emitters, the two being discussed here (Delmore *et al.* 1994), and molten glass emitters made using the silica gel method (Huett *et al.* 1995). Briefly, the ions were shown to come from the face of the deposit, and not from interfacial regions. This might be obvious in hindsight, but before these imaging measurements were made there was the distinct possibility that the ions could originate from the metal surfaces that supported and surrounded the deposits. The imaging studies demonstrated conclusively that the ions were coming from the face of the deposits, and by inference that the chemical and physical properties of the deposit determined the emitter properties of the system. The substrate (the tube which holds the deposit) served the purpose of supporting the deposit, hopefully, but not always, inertly.

The ion/neutral mass spectrometer has been used to perform a preliminary study of potassium cation emission from zeolites pressed into stainless steel tubes. The alkali metal zeolites are known to be ionic conductors, which means that they conduct electricity with cations which are mobile in the lattice, as opposed to conduction with electrons. These ion emitters are stable and intense emitters of potassium cations. At no time could any neutral species be observed which contained potassium. The only potassium species observable was the atomic cation. This demonstrates that the mobile cations in the solid phase are being desorbed as cations into the gas phase, and that this is a straight-forward example of preformed ions passing from the condensed phase into the gas phase.

We have conducted extensive studies with various perrhenate salts blended with various rare earth oxides (Delmore *et al.* 1995). We have found that the alkaline earth perrhenates are reasonably refractory compounds, and are the only perrhenate salts that give good ion emission when blended with a rare earth oxide. Ba perrhenate is the salt of choice. The best ion emitters by

far are composed of Ba perrhenate in a Eu_2O_3 or Yb_2O_3 matrix. These rare earth oxides are in the +3 oxidation state, but stable +2 oxidation states are available. It is hypothesized that the +3 oxidation states of Eu and Yb can function as mild oxidizing agents since they can be reduced to the +2 state. This in turn helps maintain rhenium as perrhenate, in which rhenium has the maximum oxidation state of +7. An alternate explanation is that the accessibility of the +2 oxidation state allows for a different crystal structure which might enhance ion emission. The Eu oxide matrix gives an order of magnitude more intensity than rare earth oxides like Nd early in the life cycle of the emitter, largely due to the fact that it can be heated to higher temperatures without depleting perrhenate. At the higher temperatures and emission currents, the lifetime of the Eu based emitter is from one to two orders of magnitude longer. This supports the hypothesis that perrhenate is being lost in the Nd host matrix, while it is preserved in the Eu based emitter. If it were related to factors such as work function, or mobility of perrhenate in the host matrix, factors which might be expected to be related to crystal structure, then it would be expected that the intensity at any given time would be different but not that the lifetimes would be so different. We feel that the evidence supports a model where pre-formed ions are sublimed from the surface (Delmore *et al.* 1995).

SIMS Applications

It has been recognized since the early days of SIMS that when an anion strikes an insulating surface, that electrostatic charging is much less of a problem than when a cation strikes the same surface (Anderson *et al.* 1969). This is because there are more secondary electrons sputtered from the surface than ions, and an electron leaving the surface causes the sample to charge positive, the same as an arriving positive ion. An arriving negative ion tends to balance the lost secondary electrons, greatly reducing the charging rate. The limitation in implementing this concept was the lack of anion guns, with the O^- gun (Anderson *et al.* 1969) the only practical one available. The mass of this ion is so light that its use has been limited. The halide guns have the threat of corroding the vacuum system, since they generally employ elemental halogen (Rachidi *et al.* 1976). Hence most primary ion guns for SIMS have employed cations, with Ar, Xe, Cs and Ga most commonly used. When insulators are to be analyzed, electron flood guns are used to balance surface charging. The balance point between the flux from the cation gun and the flux from the electron flood gun can be a problem with many instruments. This problem is much less severe with TOF-SIMS, however, since the sample can be flooded with electrons when the cation beam is turned off.

The perrhenate anion beam provides great versatility as a primary SIMS gun for the analysis of insulators, especially when combined with the technique of pulsed extraction (Appelhans *et al.* 1990). Also, the heavy mass (250 daltons) provides excellent secondary ion yields, although one-on-one comparisons of secondary ion yields are just now being conducted, and the results of the comparison are not yet published. The extraction voltage applied to the sample, which causes secondary ions to be

focused into the mass spectrometer, is reversed about 20 time per second, alternately focusing positive and then negative secondary ions into the mass spectrometer. The duty cycle between positive and negative ion extraction is adjusted to find a charge neutrality point, with ion collection times tied to this duty cycle. This has proven to be a highly efficient method for maintaining charge neutrality on insulating samples.

We have built five static SIMS instruments which employ the perrhenate anion source used with pulsed extraction, and have had remarkable success with the analysis of insulators (Delmore & Appelhans 1991; Groenewold *et al.* 1995a,b,c,d,1996; Ingram *et al.* 1995). The large perrhenate molecular anion has proven to be particularly effective at lifting adsorbate molecules from surfaces. We have analyzed molecules such as the pesticide malathion (Delmore & Appelhans 1991) directly on the surfaces of plant leaves, the extractant tri-n-butyl phosphate adsorbed on soil and rock (Groenewold *et al.* 1995a,b), the indoor air contaminant cyclohexyl amine on dust particles and miscellaneous laboratory objects (Groenewold *et al.* 1996), the degradation products of chemical warfare agents on a variety of surfaces (Ingram *et al.* 1995; Groenewold *et al.* 1995c), and the detection of inorganic complexes on carbon (Groenewold *et al.* 1995d). These analyses are but a few of the many types which these instruments have been able to accomplish.

The analysis of 'salt cake' is one example of the efficacy of the perrhenate primary ion for producing rich inorganic species information. Salt cake is a material which has formed in radioactive waste storage tanks, and there exists an important need for characterization. A synthetic salt cake was prepared minus radio nuclides to simulate actual material, to evaluate different characterization techniques (Bajic *et al.* 1995). The synthetic sample consisted primarily of sodium nitrate, with a significant quantity of nitrite and sodium nickel ferrocyanide. The composition of the sample is described in terms of the relative number of moles added (Table 1).

Table 1

Relative molar composition of synthetic salt cake, normalized to NaNO_3 .

Comonent	mole fraction
NaNO_3	1.000
NaNO_2	0.100
$\text{NaNO}_3\text{SO}_4\cdot\text{H}_2\text{O}$	0.010
$\text{Na}_2\text{NiFe}(\text{CN})_6$	0.220

The anion spectrum was particularly informative regarding inorganic species present in the sample. The most abundant ion in the anion spectrum was CN^- , and relatively abundant Na, Fe and Ni cyanide adduct ions were also readily observable at m/z 75, 108, 110, 112, 134, 136, and 138 (Figure 1; note that the Ni adducts have two major isotopes). Fe and Ni both have two cyanide adduct ions, one each for the +2 oxidation states, and one each for the +3 oxidation states. In addition to the cyanide bearing ions, nitrate/nitrite bearing species were observed at m/z 115, 131 and 147. These ions correspond to $\text{Na}(\text{NO}_2)_2^-$, $\text{Na}(\text{NO}_2)(\text{NO}_3)^-$, and $\text{Na}(\text{NO}_3)_2^-$. What is significant about the observation of these ions is that they were either low abundance, or could not be

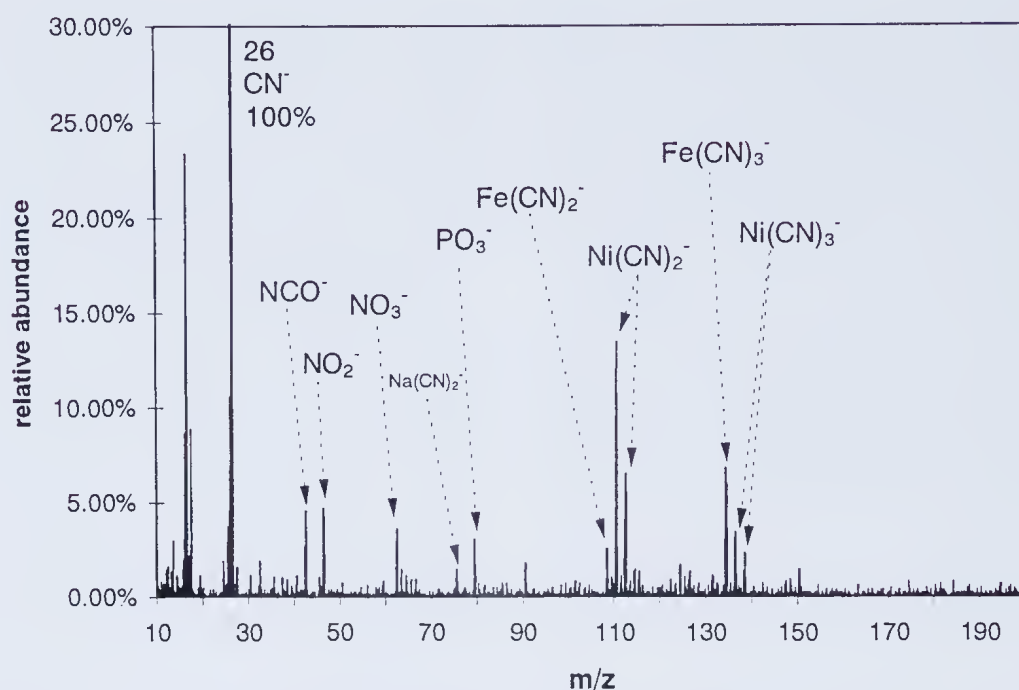


Figure 1. Anion SIMS spectrum from salt cake (described in Table 1). Note the prevalence of complex molecular species in relation to the more simple species.

observed when the sample was analyzed using a SIMS spectrometer equipped with an atomic primary ion gun (Ga^+).

Conclusions

We have studied the chemical and physical characteristics of ion emitting deposits, and have developed unique instrumentation and methods for investigating the nature of these emitters. We feel that the real high intensity "boomers," which give very high ion yields, are probably systems which form ions in the condensed phase prior to emission. While we have gained new insights into these emitters, much remains to be learned. For example, probably many other high intensity ion sources could be developed but have not yet been discovered. There is also the question as to whether europic oxide is truly an oxidizing matrix, or if the ability of this matrix to enhance perrhenate anion emission is due to some other factor. Many such research topics can be envisioned, and they only await study.

The original intent of these studies was to gain new insights into ion emitters so as to allow better isotope ratio analyses for nuclear and geologic studies. This has remained an interest, but in the process emitter systems have been discovered which emit heavy and unusual ions (in particular the perrhenate anion), that have proven to be valuable for the static SIMS analysis of heavily insulating surfaces. The perrhenate anion has proven to be particularly valuable for the analysis of partial monolayers of adsorbed contaminants on insulating surfaces.

This work also demonstrates the extent to which a scientific project can lead to new lines of study, some of which can have practical applications that could never have been predicted. The fission yield studies of 30 years ago have led us through a sequence of programs and studies which today give us the capability to measure

environmental pollutants. The common thread that allowed this to occur has been a better understanding of ion emission from hot surfaces.

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SHRIMP: Origins, impact and continuing evolution

W Compston

Research School of Earth Sciences, Australian National University, Canberra ACT 0200

Abstract

The ion microprobe SHRIMP was engendered by the need for *in situ* micro isotopic analysis of minerals relevant to research in isotope geology at RSES. It was home-built and made large to avoid the loss of transmission that accompanies small ion probes of traditional design. The presence of high quality mechanical and electronic workshops at the RSES, the experience of S W J Clement in ion optical design, the advent of new mass-analyser designs by H Matsuda, and the funding regime then enjoyed at ANU that allowed long-term and high risk projects, were each an essential component in the decision to proceed. Some details are given of the history and construction of SHRIMP I, a description of an alternative model now under construction termed SHRIMP-RG, and an account of the initial applications to isotope geoscience that have been more widely developed since. Comparison is made between the performance of SHRIMP with other methods for *in situ* isotopic analysis now available or under development.

Introduction

This is an account of one particular analytical instrument, the Sensitive High Resolution Ion MicroProbe (SHRIMP), rather than of the development of ion microprobes in general. Such a restriction is appropriate to the present symposium because the first commercial SHRIMP was manufactured for the Perth Consortium, and John de Laeter was the driving force behind it. I wish to emphasize that the development of SHRIMP from its conception to realization has been very much a team effort. Finally, history has its own uncertainties, equivalent to experimental error in analytical sciences, the main one being the recollection of exactly what did happen rather than how it was rationalized later.

Development of SHRIMP I

The need for *in situ* micro-isotopic analysis

Since about 1960, use of the electron microprobe with its *in situ* capability for elemental analysis has transformed our understanding of the geochemical relationships between coexisting minerals. However, its performance for trace elements is limited by the high x-ray background continuum, and for the light elements by the very low energy of their characteristic x-radiation. In addition, the electron microprobe cannot measure the isotopic compositions of elements such as Pb, so that it cannot give direct *in situ* age determinations.

In the late 1960s, physical-chemist C Andersen of the Applied Research Laboratories (ARL) used a small ion microprobe designed by H Liebl to develop procedures for successful *in situ* determination of concentrations for many elements. Andersen & Hinthorne (1972) used the same instrument to measure the age of fine-grained U-

rich minerals in lunar rocks. At that time, their results were disparaged by some isotope geochemists, but the possible use of *in situ* instrumental analysis was a very appealing prospect for others struggling to develop clean laboratories and to miniaturise their chemical separation procedures for analysis of the very small amounts of returned lunar samples. No chemistry or mineral separation would be required, and the ion probe itself would pre-clean the area selected for analysis. The idea of obtaining an ion microprobe at the Australian National University for the purposes of geochemistry and within-grain age determinations thus arose directly from Andersen's demonstrations.

To buy or to build?

Mainly for its promise of sensitive and rapid elemental analysis, S R Taylor proposed in early 1971 that the ANU should purchase an ARL instrument. The Bureau of Mineral Resources in Canberra indicated its willingness to help with the purchase, but the proposal was abandoned shortly afterwards due to a prohibitive rise in the cost. This might be viewed in retrospect as a fortunate escape, as the extent of secondary molecular fragments that would interfere with the required elemental ions was not realized until later. Discussion began later that year between S W J Clement and myself on the possibility of building our own high resolution instrument.

The types and abundances of secondary molecular fragments produced by sputtering depend, among other factors, on the chemistry of the target. Andersen was able to identify the main such interferences for his lunar U-rich minerals, and to correct for them by subtracting a calculable fraction of the ion beams at other masses where the particular interference dominated (the 'peak-stripping' procedure). The procedure worked well with the old and U-rich lunar minerals for which the radiogenic Pb isotopes constituted a large fraction of each Pb mass. However, when the interferences dominate the latter, as for example for young and/or U-poor zircon, a

serious magnification of experimental errors must result. In addition, how could we know that all possible isobars from any given mineral had been identified? When these complications had been fully realised, our attention turned to the possibility of obtaining an ion microprobe that could operate routinely at *high mass-resolution*, at least 5000 in the case of zircon, enough to separate nearly all the unwanted isobars.

In March 1973, in response to continued discussion, Anton Hales (first Director of the newly-established Research School of Earth Science) requested the advice of a formally-constituted RSES Ion Probe Committee comprising Taylor, S J B Reed and myself. One alternative was to buy one of the first commercially-available high resolution ion probes, which had been developed by Associated Electronic Industries by combining the highly-successful spark-source mass spectrograph, the MS7, with the primary probe-forming column developed by I W Drummond and J W P Long of Cambridge University. One of these instruments already had been ordered by the University of Chicago (J V Smith) and the University of Cambridge (J W P Long) for geological applications. The other alternative was to design and build our own ion probe in-house, including the employment of S W J Clement for the ion optical and engineering design as an essential ingredient.

Clement and I had become concerned that the sensitivity of the AEI and other small commercial machines then under development (Micromass, Cameca) would be too low at high resolution for effective use in U-Pb age determination. There was no doubt that the MS7 could achieve 5000 R, but we realized that like all other small mass-analyzers, it did so by the use of very narrow slits both at the source and the collector. The narrow source slit reduced the transmitted secondary ion beam and hence reduced the sensitivity for trace-element detection. The narrow collector slit removed the 'flat-top' from the mass spectral peaks that experience with thermal ionization mass spectrometry showed to be essential for accurate quantitative measurements. There was a fundamental trade-off here, sensitivity for high resolution.

The field of beam transport theory, which Clement had used in his PhD project, was obviously relevant for an optimal design. It was also clear that the use of a wide source slit for higher sensitivity at high mass-resolution would demand a much larger magnet than any available from mass spectrometer manufacturers. The latter (very sensibly) wished to make their ion probes as an assembly of mass-spectrometer components that had been developed already (and debugged) for other purposes, typified by the adaptation of the MS7 spark-source mass spectrograph. Manufacturers also aimed for small instruments to lower the price and reduce floor space. We felt that a custom-designed ion probe had to be superior.

Design, Personnel and Construction

Following support by Faculty Board, The RSES Director (A Hales) approved the proposal to build the ion probe in-house in late 1973. The decision was influenced by the favourable infrastructure for instrument construction that was the School's heritage from its former presence within the Research School of Physical Sciences.

RSES had well-equipped and expert machine and electronics shops, accustomed to the design and manufacture of new apparatus and much larger than found in contemporary geology departments elsewhere. The high-risk nature of the project was recognized from the outset. We hoped to progress with capital costs spread over a five-year period. The costs of establishment salaries were not included.

The initial working group comprised S Clement, F Burden (mechanical), N Schram (electronics), D Millar (technical officer) and myself, with Professor G Newstead from the Department of Engineering Physics joining in early 1974 for magnet design and D Kerr of the BMR for computer-control in 1975. This group met each month from 1975 to ensure a full exchange of information, with reports to Faculty Board.

The Matsuda mass-analyser. Clement arrived in early 1974 to make the detailed design. The key part of the instrument was the mass-analyzer, which needed to give simultaneous high resolution and high sensitivity. Clement had completed an original analysis for a double-focussing mass analyzer by mid-1974, but then H Matsuda of Osaka University published his most relevant paper on sector mass-analyzer design (Matsuda 1974). We needed a design that minimized the complex image-aberrations inescapably present in ion optical systems, as well as one that seemed to lie within our practical capabilities such as employing a cylindrical rather than toroidal electrostatic analyzer (ESA). Matsuda (1974) addressed exactly those conditions. He considered the ion optics of sector mass analyzers as an integrated whole, as distinct from aberration-free individual components. Just as the energy-dispersion of the ESA, which as energy-spread represents a first-order aberration of the image, is adjusted to be equal but opposite to that in the magnet to obtain a double-focussing system, Matsuda arranged the various ion optical components so that their second-order aberration coefficients also cancelled each other. An essential part of this was the introduction of an electrostatic quadrupole lens (the 'Matsuda' lens) between the ESA and magnet. There was also curvature in the z-direction of the entrance edges to the ESA plates. For the particular Matsuda design that we favoured, the theoretical image-aberrations would sum to ≤ 6 microns for the magnet turning radius of 1 metre (which we considered to be the largest that we could manage) and for angular divergences and energy-window of ± 0.005 . Clement confirmed Matsuda's calculations using an independent computer program (from C Stevens of the Argonne Laboratory at the University of Chicago) based on phase-space transformations. We concluded that there could be no better design for our purpose, and adopted it henceforth.

Tribulations of fabrication. The 6 tonne magnet was powered without pole-pieces in late 1976. Each pole-piece was intended to be an assembly of five insulated segments of silicon steel but this material was abandoned after very slow delivery followed by external handling mistakes. They were made instead of soft-iron segments machined and annealed in-house with great care. In 1979, segments laminated from transformer shim were tried to permit faster field switching. This indeed was the case but the refocussed image at the collector appeared to be variable in quality, which may or may not

have been due to the laminations (see below), and we returned to the solid segments.

Practice can never be quite as good as theory. Matsuda (1974) envisioned perfectly uniform magnetic and electric fields and perfect geometry, but it is hard to achieve perfection with real materials and real engineering. A further example concerned with the magnet will illustrate this. No magnetic field terminates exactly at the edges of the pole-pieces; rather, it falls off sharply over a finite distance beyond them so that it is necessary to determine the position of an *effective* field boundary. In practice, the magnet for small sector instruments is traversed on rails at right angles to the line joining the source and collector slits until the narrowest image is found empirically. The shape and weight of our ion probe magnet did not allow it to be moved, so instead the collector had to be traversed along the beam-line to find the exact image point. However, the image quality was found to depend strongly on the particular mass collected, and also on the preceding values for the magnetic field.

These observations produced the lowest points of morale in the project. What was wrong with the magnet? No such effects were previously described, although we had noticed with thermal ionization instruments that Sr and Pb ions needed slightly different positions of the magnet for the best refocussing. The discovery that the image point moved in reproducibly with decreasing field when the magnetic field was kept in a fixed cycle of steps saved the situation. The collector could then be driven under computer control to a preset optimum position for each required mass. This remains our solution to the problem. We learned later that at least one manufacturer corrected the effect when making wide-range scans at high mass-resolution by an in-built computer-driven einzel lens. This was not publicised as if the need for such a correction was an admission of deficiency. We have since found that the size of the effect (several mm per 50 daltons) can vary with different SHRIMP magnet designs and may even be reversed. The effect might be due to very slight change in the pole-gap width as the field is changed, or to slight changes in field distribution due to changes in flux-density in the yoke, or both.

The fabrication of the ESA vacuum housing and 1.3 m radius electrodes was subcontracted to the Bendigo Ordnance Factory in late 1975, and delivered in early 1977. J Coles was appointed to assist in final assembly and testing of the ion probe in late 1977, and to develop its application to light element stable isotope ratios. The first detailed report on the testing of the ion probe mass-analyser using a thermal ionization source appeared in the Annual Report of the Research School of Earth Sciences (Clement *et al.* 1978). The first secondary ions generated by sputtering were produced a year later (Clement *et al.* 1979).

First geological applications

S and Pb isotopes in sulfides. Using an Ar^+ primary beam, the first geological tests of the instrument were for Pb^+ isotopic ratios from Broken Hill galena by ion-counting (Coles *et al.* 1980). The beam was very stable and the results precise. Tests were extended to the isotopically variable Mississippi Valley sulfides and to the use of

large PbS^- and PbS_2^- beams measured via the Faraday cup, with peak-stripping of the sulfur isotopes. Significant variations both in Pb and S isotopic ratios were found, but the work was never submitted to any refereed scientific journals. S isotopic ratios in galena, measured both as S^+ by ion-counting and as S^- by the Faraday cup, were also demonstrated.

Ti isotopic composition of terrestrial minerals. With the discovery of small nucleogenic ^{50}Ti isotopic anomalies in Ca-Al-rich chondrites using thermal ionization mass-spectrometry, one of the first ion probe applications to be examined was the accurate and precise measurement of Ti isotopes in several terrestrial minerals (Compston *et al.* 1981). The crucial need for accurately-known and constant values for the dead-time of the detector and counting system was encountered first-hand, and also the presence of systematic differences in mass-discrimination in the sputtering of different mineral species.

U-Pb dating. The potential of within-grain analysis for determining the crystallization history of zircons had been appreciated since the early 1970s, following discoveries using conventional dating techniques that old grains had preserved their ages through Alpine-age granulite-facies metamorphism, and that xenocrysts in some granites had survived fusion temperatures. I S Williams, who had analysed zircons and other U-rich minerals by the conventional method, was appointed at RSES in 1981 to participate in the hoped-for use of SHRIMP for this purpose. We sought to find an analytical method that would allow us to generate realistic values for the radiogenic $^{207}\text{Pb}/^{235}\text{U}$ and $^{206}\text{Pb}/^{238}\text{U}$ per analysed spot, that could be plotted on the Concordia diagram.

The particular problem for zircon was the need to determine $^{206}\text{Pb}/^{238}\text{U}$ reliably, as it was quickly established that its $^{207}\text{Pb}/^{206}\text{Pb}$ as measured using sputtered secondary ions agreed to within ion counting statistics with that measured by thermal ionization. In great contrast, the observed Pb^+/U^+ from sputtering and mass-analysis was about three times larger than the $^{206}\text{Pb}/^{238}\text{U}$ in the target for zircons of known age, with repeat analyses from grains having the same age varying over a 10% range. The previous work by Andersen & Hinthorne (1973) on transforming their measured ion probe data into chemical concentrations, combined with our practice from thermal ionization of normalizing to a fixed ratio to correct for variable discrimination, led us to an empirical but successful procedure. Reasonable linear correlations were found between the observed Pb^+/U^+ and the observed UO^+/U^+ in zircons that have the identical age (Williams *et al.* 1981). This allowed us to correct Pb^+/U^+ as measured for variable discrimination by normalizing to a fixed value for UO^+/U^+ , then to use the corrected Pb^+/U^+ of a concurrently measured zircon of known age as a comparison-standard. With continued development, the procedure now allows us to measure the $^{206}\text{Pb}/^{238}\text{U}$ ages of very young zircons with sufficient accuracy and precision both to compete with the conventional method and to detect inherited zircons as whole grains and inclusions that are not otherwise detected (Compston & Williams 1992).

Impact of Shrimp in Isotope Geoscience

There is no doubt that zircon U-Th-Pb measurement has been the dominant use of SHRIMP so far. Of a minimum

of ca. 150 articles that have appeared in refereed research journals to the end of 1995, only ca. 15 % deal with isotope ratios of the 'light' elements (S, Ti, Mg). The remainder have used zircon geochronology for geological reconnaissance or to test various geological hypotheses. However, the 15 % light element applications demonstrate that SHRIMP can be used over the whole nuclidic range, and the dominance of zircon studies simply reflects our current perceptions of what has been the most rewarding scientifically. This balance may change in the future.

We regard the following projects as originating a number of important types of applications of SHRIMP to the earth sciences that have been used widely and developed further.

Accurate age measurements on terrestrial zircons. Antarctic zircons, previously dated using the original (small) ARL ion probe and its peak-stripping methods for isobaric interferences, were reanalysed by SHRIMP. The ages found were wholly consistent with geological constraints, and previously contentious results were shown to be an artefact of uncorrected isobaric interferences in the ARL data (Williams *et al.* 1982; Williams *et al.* 1983).

Ages of zircon overgrowths in polymetamorphic episodes. The main reason for the development of SHRIMP was *in situ* microanalysis, with the prospect of detecting age-differences between different growth-zones within a single mineral. This capability was first illustrated for zircons from the Archaean Napier Complex in Antarctica and in zircon xenocrysts from Palaeozoic granites in Eastern Australia (Williams *et al.* 1981, 1982). Unsupported radiogenic Pb within a single zircon was observed in high-grade gneiss at Mt Sones (Williams *et al.* 1983, 1984), and the growth at high metamorphic grade of characteristically low-Th/U zircon rims around Proterozoic grains was documented first in the Scandinavian Caledonides (Williams & Claesson, 1987).

***In situ* age measurements on lunar zircons and initial Pb in lunar feldspars.** Ion probe geochronology started and continued for 10 years on lunar zircons that have been discovered by diligent search of many lunar thin-sections by Lunar Sample Curator Charles Meyer (Compston *et al.* 1983). Serial lunar magmatism since 4.35 Ga has been established. Meteoritic zircons have been dated also (Ireland & Wlotzka 1992). More recently, the high sensitivity and within-grain targeting capability of SHRIMP showed that the extremely radiogenic composition of Ba-rich feldspars in lunar felsites is an original magmatic characteristic rather than a product of the 'terminal lunar cataclysm' (Compston *et al.* 1988; Compston *et al.* 1991).

Oldest-known terrestrial zircons. This discovery arose from our use of the age-spectra of detrital zircons in Archaean sediments to explore the ages and nature of their source rocks (Froude *et al.* 1983). It generated studies of detrital zircon ages in other Archaean metasediments, and of trace-elements, especially REE, in inclusions within the old zircons (Maas *et al.* 1992) that bear on the nature of the primary zircon sources.

The dating of young zircons. Palaeozoic zircons were at first considered to be too young for ion probe dating

because the amount of ^{207}Pb is usually too low to obtain useful $^{207}\text{Pb}/^{206}\text{Pb}$ ages. Consequently, the dating of young grains by ion probe must rest mainly on their $^{206}\text{Pb}/^{238}\text{U}$ ages, which in turn are limited by the ability to control the variable discrimination of ^{206}Pb relative to ^{238}U during sputtering and secondary ion extraction. Mainly for this reason, we obtained and analysed zircons from the collection made by R Ross and others from bentonites in the British Ordovician stratotypes (Compston *et al.* 1982). The project has developed into continuing applications of SHRIMP to the definition of the geological time-scale (Compston & Williams 1992; Compston *et al.* 1992), with the realization that some of the zircon samples used for conventional time-scale dating were probably composite in age due to inheritance, a point hotly disputed and now in the process of resolution. The capability of SHRIMP to determine extremely young zircon ages was first illustrated by analyses of 2 Ma-old zircons from the western Himalaya (Zeitler *et al.* 1989).

Terrane mapping in Archaean gneisses. The high blocking-temperature of zircon means that intense deformation and repeated metamorphism does not erase earlier zircon ages in gneisses that contain multiple age components, which in many instances allows their detailed history to be unravelled in a single sample. This was evident for the Napier Complex (Williams *et al.* 1982), and was used to decipher the history of the Narryer Gneiss terrane (Kinny *et al.* 1990; Nutman *et al.* 1991) during the search for intact 4.2 Ga rocks. Our study of the Narryer region has shown clearly that correlations between isolated exposures of gneiss cannot be made reliably without zircon geochronology. Currently, the oldest terrestrial rock known is the 4.0 Ga Acasta gneiss in Canada, first indicated as very old by thermal ionization mass-spectrometry then determined accurately as 4.0 Ga by SHRIMP (Bowring *et al.* 1989).

SHRIMP dating of other U-bearing minerals. The first lunar paper (Compston *et al.* 1984) also included the essential analytical and data-reduction procedures for zircon ion-probe work that, with various refinements, we continue to use today. The same correction method for variable discrimination in zircon analysis has been applied successfully to a number of other U-bearing minerals; perovskite (Compston *et al.* 1985), and baddeleyite, monazite, titanite and rutile (Camacho *et al.* 1993).

***In situ* Hf isotopic analysis.** The potential for hafnium as a radiogenic isotope fingerprint is well-known from thermal ionization mass-spectrometry, but Hf is a difficult element to separate chemically and to mass-analyze with the necessary precision. Because of the high Hf contents of zircons, an early reconnaissance study of the potential of SHRIMP for Hf isotopic analysis was made, with encouraging results (Compston *et al.* 1982; Kinny *et al.* 1991). Mathematical procedures for peak-stripping were developed to correct for hydride, oxide, Lu and Yb isobars, which cannot be mass-resolved by SHRIMP II without losing sensitivity. Further analyses of Hf have been deferred pending the development of the SHRIMP-RG and/or the availability of the multicollector for SHRIMP II.

Isotopic mapping of trace-element distribution within minerals. With the advent of the computer-controlled sample-stage in SHRIMP II, it has been possible to construct

detailed maps of the spatial distribution of any nuclidic or molecular secondary ion at high mass-resolution (Clement *et al.* 1992). This facility has been combined with imaging by back-scattered electrons and cathodoluminescence using the electron microscope to obtain very powerful targetting and interpretive information (Williams *et al.* 1995).

Depth-profiling using SHRIMP. The lens configuration of the primary-beam focusing column was designed originally for two-stage demagnification of the duoplasmatron extraction-aperture to produce the ca. 20 μm probe itself. However, the probe was plagued by a low-intensity but wide halo that caused a slow release of surface-related common Pb during analysis. Initially, as an experiment, it was modified to implement 'Köhler illumination' (Compston *et al.* 1983). This was successful; the probe now had a sharply-defined edge plus a highly-uniform ion-density within the sputtered area. It was then realized that 'Köhler illumination' had an advantage over spot-rastering for depth-profiling; it gave 'parallel' information over the full width of the spot rather than 'serial' as in rastering, which means a much higher sensitivity per second. In addition, it removed the need for the very small probe diameter required for depth-profiling by rastering.

Depth-profiling in this way was first employed in experiments on the diffusion of radiogenic Pb from the (high-U) SL3 zircon standard (Williams *et al.* 1988). Diffusion was induced, holding the samples at constant high temperature under hydrothermal conditions, and profiles for the escape of Pb, U and Th were determined. Results for diffusion coefficients were not then reported because it was realized that the process was not pure volume-diffusion. It was found that annealing of the samples prior to the experiments failed to remove zones of structural breakdown due to radiation damage. The work has been repeated recently using the low-U zircon SL13 and with improved control and documentation (Lee *et al.* 1995).

Ti and Mg isotopic anomalies in meteoritic minerals. Small isotopic anomalies in ^{50}Ti observed using thermal ionization in bulk refractory inclusions in carbonaceous chondrites were transformed into huge anomalies, from 2.0 % to -4.0 %, when the carrier mineral hibonite was selectively probed (Ireland *et al.* 1985). Mg isotopic analysis of the same hibonites revealed the presence of excess ^{26}Mg , attributable to *in situ* decay of ^{26}Al in some grains, ranging up to more than 1000 % in one instance (Ireland & Compston, 1987).

***In situ* S isotope analysis as an isotopic fingerprint.** Detailed SHRIMP analyses of different S-bearing mineral species confirmed that isotopic discrimination during sputtering is controlled mainly by the crystal bond-strengths, and that accurate differences in S isotopic composition can be measured relative to standards of the same mineral-type (Eldridge *et al.* 1985; Eldridge *et al.* 1987). The established techniques were first tested by applications to fine-grained sulfide ores from Mt Isa (Australia) and the classical ore deposits at Rammelsberg (W Germany), demonstrating that different generations of sulfides of the same species may be precipitated and co-exist without any isotopic equilibration between younger and older despite superposed metamorphism.

Future Developments

The continued development of SHRIMP is subject to the possibility that it might be made redundant overnight by the arrival of some new instrumental technique that is both better and much cheaper. I am aware of two micro-techniques that have been predicted as substitutes for SHRIMP. These are accelerator mass spectrometry (AMS) and laser-sampling, inductively-coupled plasma ionization mass-spectrometry (ICPMS).

Accelerator mass spectrometry

AMS for trace-element and isotope ratios is currently being developed in Australia at CSIRO, North Ryde, under the project name AUSTRALIS (Sie & Suter 1994). It involves the use of sputtering to take a continuous micro-sample just as SHRIMP does, but it uses a quite different method of dealing with isobaric interferences. Negative secondary ions of the one nominal mass are selected, then accelerated by several MeV in a tandem van der Graaf accelerator. At the positive high-voltage terminal, they are then passed through a column of Ar gas at low pressure, which does two things; it strips up to several electrons from the negative atomic ions to form multiply-charged positive atomic ions, and it ruptures molecular ions into their constituent atoms in addition to stripping off electrons. As a result, all molecular ions are destroyed so the problem of molecular isobars vanishes. The positive ion beam is then mass-analysed at low resolution.

AUSTRALIS is larger, more complex and more expensive than SHRIMP. In addition, it is one of several projects at North Ryde that will share use of the tandem accelerator, so its capacity for geological analysis will be constrained. There will be the need to correct for variable elemental discrimination during sputtering, because the collected Pb^+/U^+ cannot be normalized to the same UO^+/U^+ in the absence of molecular ions. Only negative secondary ions can be used.

Previous AMS experience has concentrated greatly on low counting-rates, and the use of sophisticated proportional counters that allow each ion to be identified from its charge-state and momentum which gives AMS its unique power for ultra-low trace-elements. In contrast with this, the U-Pb, Rb-Sr, Nd-Sm and oxygen isotope applications for geology demand the use of very high count-rates, to realise enough precision in a reasonable analytical time. AMS will thus have the same high count-rate linearity challenge in the detector as SHRIMP, and rather than detecting ions of 10 keV energy, AMS will need to handle ion energy of several MeV.

Laser-sampling, inductively-coupled plasma ionization mass-spectrometry

At the recent meeting of the ANZSMS in Sydney, G Hieftje from the Department of Chemistry, University of Indiana assessed the present and future status of 'Atomic Mass Spectrometry' (Burgoyne *et al.* 1995). He addressed the question of just how good ICPMS is, as presently available commercially, for making quantitative fast determinations of all the elements and isotopes.

For *in situ* micro-analysis, a succession of pulsed laser shots is fired to ablate the target. This ablated material is swept away in a stream of gas, usually He, then the gas

plus suspended particulate sample introduced to the inductively-coupled plasma to be ionized. Ionization is done with great efficiency hence high sensitivity could be available. Then the ions are extracted and mass-analyzed either on a fast quadrupole analyzer for wide mass-range and speed, or on a double-focussing sector analyzer with multicollector if a relatively small mass range is sufficient.

Hieftje emphasized several practical problems. The laser gives a non-continuous supply of the sample. The intensities of the sample ions rapidly rise with the start of the pulse then decline, and all the isotope and elemental ratios must be measured while this is happening. Because quadrupole mass-analysers measure masses in sequence, the influence of a variable sample signal is difficult to eliminate, and therefore use a time-of-flight mass-analyser which analyzes ions of all masses formed during the same short time-interval was necessary. Currently, the TOF analyser has an efficiency-problem; the heavy ions must travel to the detector before taking another laser pulse. To improve this even to 10% efficient duty-cycle, complex electronic timing and electric field sweeps are necessary. Irrespective of the mass-analyser, isobaric interferences remain even using plasma-ionization. Oxides are present for many elements. The exact species must be known and peak-stripping used if the mass-analyser operates at low resolution, or a high resolution mass-analyser should be used. There are also matrix-effects attributed to space-charge dispersion in high density beam-waists in the plasma; the light ions are spread more than the heavy ions. Overall, Hieftje made the point that present ICPMS instruments have serious deficiencies and that it might be 10 years before the necessary control on TOF analysers has been perfected.

The above problems are greatly reduced if instrumental needs can be restricted to isotopic ratios of single elements within the limited mass-range of multi-collector sector analyzers. However, there is one ultimate comparison that should be made between the SHRIMP ion microprobe and all ICPMS instruments, laser-sampling or otherwise. Which method of analysis has the greater intrinsic sensitivity? The fundamental definition of sensitivity for a given element is its *useful yield*, the ratio of ions collected for analysis per second to the number of atoms of that element consumed per second by the sampling process. Here, SHRIMP remains well ahead of ICPMS. For SHRIMP I at $\geq 5000R$, the useful yield for Pb in zircon was measured approximately as 0.7% (Compston & Williams, unpublished), and more accurately for SHRIMP II at $\geq 1.5\%$ (J W K Lee & I S Williams, *pers. comm.*). The only published ICPMS value known to me is 0.22 % for Pb in a standard glass (Walder *et al.* 1993). Even lower values are reported verbally for Pb in zircon, 0.14% (P. Turner, *pers. comm.*). It is therefore quite clear that the *total* sensitivity found for trace elements using laser-sampling ICPMS has been obtained by the use of much greater amounts of sample than SHRIMP. This is consistent with the multiple laser shots used per analysis as well as the hemispherical shape of the laser pits (e.g. 20 μm diameter and 20 μm deep), as compared with single 20 x 25 μm elliptical spots using SHRIMP that are typically only 1 μm deep.

Recent theoretical advances in sector mass analyser design

Advances in ion optical theory have been made by H Matsuda, whose 1974 design we employed for SHRIMP I and II. Matsuda (1990) has now shown that it is possible to design families of double-focussing sector mass-analysers that have strong demagnification of the final image without an equivalent reduction in the mass-dispersion. This means that for a mass-analyser of a given size ('size' means turning radius of the magnet), the mass-resolution at a given object-slit width (which sets the sensitivity) can be increased by a large factor. The particular design selected for the SHRIMP-RG will operate routinely at the same sensitivity as SHRIMP II, but with 4x greater mass-resolution. That in turn means that a number of new and important types of geochemical analyses, not practical for SHRIMP II, could be undertaken using an ion probe based on the post-1990 design.

There are some constraints that accompany the new design. One is that multiple collection can never be used, because the beam must be sent first through the mass-dispersing magnet rather than first through the energy-analyser. This arrangement is known as 'reverse-geometry'. Only one selected mass at a time can be transmitted through the energy analyser to the collector slit, thereby limiting the collection of data to the intrinsic inefficiency of a single collector. On the other hand, the latter has the virtues of equal gain for all masses, simplicity and cheapness. In addition, reverse-geometry is well-known to give much higher abundance-sensitivity than forward-geometry *i.e.* the background of scattered ions will be very small so that low abundance peaks can be measured more accurately.

The new design must be well-corrected for image-aberrations to give highly demagnified images of good quality. The present SHRIMP IIs have low values for all 2nd order aberration coefficients, but the new design requires that several 3rd order coefficients must be low also. As in SHRIMP II, the design itself incorporates the means of nulling the necessary image aberrations through its particular selection of ion optical parameters. We therefore consider that the attainment of good focussing in the new design will be no more difficult than in SHRIMP II.

Practical design problems for a new model SHRIMP

A constraint in the new design is the need for a much wider pole-face area than that used in the SHRIMP II magnet. At its widest, the secondary ion beam will diverge to ± 120 mm within the sector magnet compared with ± 30 mm in SHRIMP II. This places a greater demand on the design and engineering of the magnet, especially for the laminated pole-pieces that are necessary for fast field-switching.

The question arises of whether the theoretical performance of the new designs can be made in practice, bearing in mind the imperfections of fabrication, variable magnetic properties of iron, and small misalignment of components. The same concerns were held for SHRIMP I but proved groundless. In addition, the manufacturer JEOL has successfully produced more than 100 small double-focussing mass spectrometers based on one of Matsuda's new designs, which gives confidence that the theoretical performance can be achieved. We are satisfied

therefore that the necessary low image-aberrations will be achieved at the same level of accuracy in machining and alignment of ion optical components as used in the manufacture of SHRIMP II. Nevertheless we will take the precaution of including at least one ion optical stigmator to compensate empirically for image imperfections.

Advantages of the SHRIMP-RG

The principal benefit of the SHRIMP-RG would be the removal of isobars, such as hydrides of the heavier elements, that trouble or disallow a number of important geochemical applications. Examples are listed below but there will be many more. Discoveries in research cannot be predicted. In general, mass-resolution should be viewed as a commodity that cannot be overdone. In addition, SHRIMP-RG could be operated with a very wide source slit for other applications, such as stable isotope analysis, that do not demand high mass resolution but are especially susceptible to variable mass discrimination. Discrimination in the secondary ion mass-analyser cannot occur in the absence of beam truncation. In SHRIMP II, truncation occurs both at the source slit (at least 10 % of the beam at resolution 5500) and at other apertures during the transfer of ions from the analysed spot to the source slit. SHRIMP-RG offers the opportunity of improved phase-space matching between the mass-analyser and the analysed spot. If the present truncations can be avoided totally, only the sputtering process itself would remain to cause variable discrimination.

Some geological applications for SHRIMP-RG

Interference between Sr isotopes and Ca isotope dimers, such as $^{44}\text{Ca}^{43}\text{Ca}$ with ^{87}Sr ($m/\Delta m$ of 16000) discourage serious $^{87}\text{Sr}/^{86}\text{Sr}$ fingerprint studies for the above and other Ca rich minerals. Sr isotope 'chemostratigraphy' is plagued by ambiguity caused by diagenetic alteration. Using whole rock samples, it is rarely clear whether a genuine shift in seawater isotope composition has been discovered in a stratigraphic sequence or a zone of later fluid alteration. Ion probe analysis will reveal diagenetic changes in many cases through their variable effects on a 10 micron spatial scale, and preserved areas should be identified.

^{40}K - ^{40}Ca dating of K-rich minerals

There is a moderate prospect that radiogenic ^{40}Ca will be retained more strongly than ^{40}Ar during cooling after igneous emplacement or metamorphism, so that ^{40}K - ^{40}Ca ages of mica and K-feldspar would contribute to cooling history studies. The problem will be to find minerals in which the radiogenic ^{40}Ca is not diluted by common Ca. There are good prospects that *in situ* 10 μm scale analyses will be better in this respect than bulk mineral separates. The very high abundance-sensitivity of SHRIMP-RG would minimize scattering from the adjacent intense ^{39}K peak. In addition, it would be possible to resolve ^{40}K from ^{40}Ca ($m/\Delta m$ of 28000) during analysis so that the ratio $^{40}\text{Ca} / ^{44}\text{Ca}$ would be a direct measure of the radiogenic enrichment without peak-stripping of K isotopes.

^{147}Sm - ^{143}Nd dating and ^{143}Nd isotope labelling of REE-rich minerals. There are at least two problems with ion probe analysis for the above; the need for maximum sensitivity to amass enough counts for worthwhile precision,

and the need for minimum peak-stripping of isobars to keep the analysis process simple. Some minerals such as perovskite have no obvious isobaric interferences other than hydrides, which SHRIMP-RG would remove at resolution 25000. More complex interferences must be expected for silicates and phosphates.

Removal of $^{206}\text{Pb}^1\text{H}$ from ^{207}Pb in the dating of hydrous minerals

The variable water content of pitchblende or any other U-rich hydrous mineral inhibits us from attempting to date such minerals at present. Peak-stripping is unreliable because mass 209 might be occupied by ^{209}Bi as well as $^{208}\text{Pb}^1\text{H}$. The ratio of $^{90}\text{Zr}^1\text{H} / ^{90}\text{Zr}$ could be used for Zr-bearing minerals as shown by Long & Hinton (1984), but this requires very large mass jumps during data-collection. Although large jumps might be practical on SHRIMP II when the laminated magnet poles are fitted, it would be far better to remove the hydrides at resolution 29000 which should be possible for SHRIMP-RG with some loss of sensitivity.

Removal of hydrides in Hf isotope ratio measurement

At present, peak-stripping must be used to remove ^{18}O , Yb, Lu and hydrides. Moreover, the hydrides of Yb and Lu differ in proportion to that of Hf. There is only one independent Hf isotope ratio left after the stripping to judge the veracity of the process, which is dangerous. The absence of the need to strip hydrides would be an enormous advantage, and it would be routinely possible to operate SHRIMP-RG at the necessary 22000 mass-resolution.

Easy separation of light REE oxides from heavier REE metal ions

Our REE measurement procedure is presently limited by the need to select the best mass-channels to avoid oxide overlaps. The routine operating resolution for SHRIMP-RG would remove these and other isobaric interferences that will arise when different minerals and REE levels are attempted. When trace-elements are present at the ppb level, many new possibilities exist for isobaric interferences that can be neglected at the ppm level. Examples are low abundance combinations of very light nuclides (e.g. boron) which have nuclidic mass 'surpluses' with oxides of heavier nuclides which have mass deficiencies. If geochemistry is to examine trace-elements in minerals at such levels, that problem must be faced.

Meteoritic isotope anomalies

SHRIMP-RG could resolve isobars in the Fe-group of elements, such as ^{58}Ni and ^{58}Fe , which opens the way for specialised cosmogenic isotope studies in addition to high-quality terrestrial geochemical/isotope analyses.

Concluding Remarks

A new Australian manufacturing company now exists to build SHRIMPs, Australian Scientific Instruments (ASI), in response to several requests made to the ANU for commercial sales. I wish to acknowledge here the very important role played by John de Laeter in precipitating our decision to participate in this commercial venture.

De Laeter formed the view that more than one SHRIMP was needed in Australia; one should also be located in Perth, for geological research at two Universities and to aid geological mapping by the State Geological Survey and by the mining industry. He also believed, and stated persuasively, that he could raise the necessary money for its purchase. At the same time, the demand for access to the ANU SHRIMP had become excessive, both from internal ANU projects, from visiting scientists and from the Commonwealth Bureau of Mineral Resources. It became clear that a second and hopefully improved ANU SHRIMP could be built as a commercial prototype, followed by manufacture by ASI from this prototype and with the Perth Consortium led by John de Laeter as the first customer. Happily, this desirable course of events came to pass.

Acknowledgements: I thank S W J Clement, T R Ireland, I S Williams, and S Sie for comments on various parts of the manuscript.

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Zircons: What we need to know

R T Pidgeon

School of Applied Geology, Curtin University of Technology, Perth, WA 6001

Abstract

The SHRIMP ion microprobe provides a new and exciting capability for determining U-Pb ages on parts of complex zircons. This opens up new opportunities for solving some equally complex geological problems, but this will depend on an understanding of the geological significance of the internal structures of the zircons, which is the key to the interpretation of the SHRIMP ages. CL imagery, HF etching, SEM imagery, X-ray and vibrational techniques for resolving zircon internal structures and crystallinity on a micro-scale are discussed.

Introduction

It is said that major advances in technology introduce as many new problems as they solve. Such may yet be the case for the new breed of high-resolution high-sensitivity micro-isotopic analytical instruments of which SHRIMP is the forerunner. SHRIMP has a broad analytical capability but was conceived primarily for the purpose of analysing U-Th-Pb isotopic systems of micro-areas of common uranium-bearing minerals of which zircon is the prime example. SHRIMP was made at a time of rapid improvement in conventional geochronology, particularly in the techniques for measuring zircons on a scale of single crystals or parts of crystals involving high precision mass spectrometric analysis of tens of picograms of Pb with blanks expressed as numbers of atoms. At this time, in the late 1970s, a wealth of knowledge was available for the mineral zircon. For example the breakdown of the zircon structure under radiation, the relationship between isotopic stability and crystallinity, and the ability of crystallised zircon to resist dissolution under magmatic conditions and to retain an isotopic memory of its pre-magmatic age, were well known. It is with this last aspect that the first major advantage of SHRIMP micro-analysis became apparent. This is its ability to measure directly the age and chemical composition of cores of ancient zircon (e.g. Williams 1992) encased in a mantle of younger magmatic zircon and then to determine the age of the zircon mantle. Such a feat is impractical using conventional technology and this alone signals that the scale of isotopic analysis and age determinations of zircons and other uranium-bearing minerals has changed forever. From now on, the frontier of zircon geochronology is within individual zircon grains. Where zircons are uniformly the same age, for example in a rapidly crystallising felsic magma, there may be no advantage in making SHRIMP analyses on small areas of zircon crystals. However, it is well known that zircons can have complex structures which are presently incompletely understood, but which are thought to reflect events in their geological history. SHRIMP analytical spots can be located on these structures once they are

identified. An example of such a grain is contained in Figure 1. The grain pictured has a complex structure consisting of a crystalline core surrounded by an oscillatory zoned rim. What we need to know now is the geological significance of these structures, so we can interpret SHRIMP U-Pb ages and the U-Th-Zr chemistry of cores and rims of such grains in terms of geological processes. We also need to have further information about the stability of zircon in a variety of geological environments.

Zircon microstructures

Chemical and structural inhomogeneities in zircons, such as oscillatory zoning, have been known for many years. What is happening at present is that techniques are being developed and improved for the purpose of highlighting the internal structures of zircons so they can be studied in detail prior to analysis by the SHRIMP. The capabilities of some of the variety of techniques used for this purpose are as follows.

Cathodoluminescence (CL) imagery is possibly the most popular technique for examining the internal structures of zircons. Cathodoluminescence is the light emitted from semi conductor or insulator material when an electron beam creates electron hole pairs which then recombine to emit light in the wavelength range from the ultra-violet to the near infrared (200-2000 nm). Although the controls of the CL spectra are not well known, it has been proposed that concentrations of some trace constituents are the determining factors. In zircons, Dy³⁺ is considered to be the principal spectral factor though other constituents such as Sm³⁺, Eu²⁺, Tb³⁺, and Y³⁺ may also be CL emitters (e.g. Hanchar & Miller 1993). The application of cathodoluminescence in highlighting micro-structures of magmatic zircons has been demonstrated by Vavra (1994).

Spectral cathodoluminescence (the analysis of the CL light spectrum) also has interesting possibilities for investigating the chemistry and structure of zircons on a micro-scale (e.g. Koschek and Lork, 1992) but up till now has been little used.

Back scattered electron imaging (BSE) reveals contrasts in average atomic number of regions of a phase; the

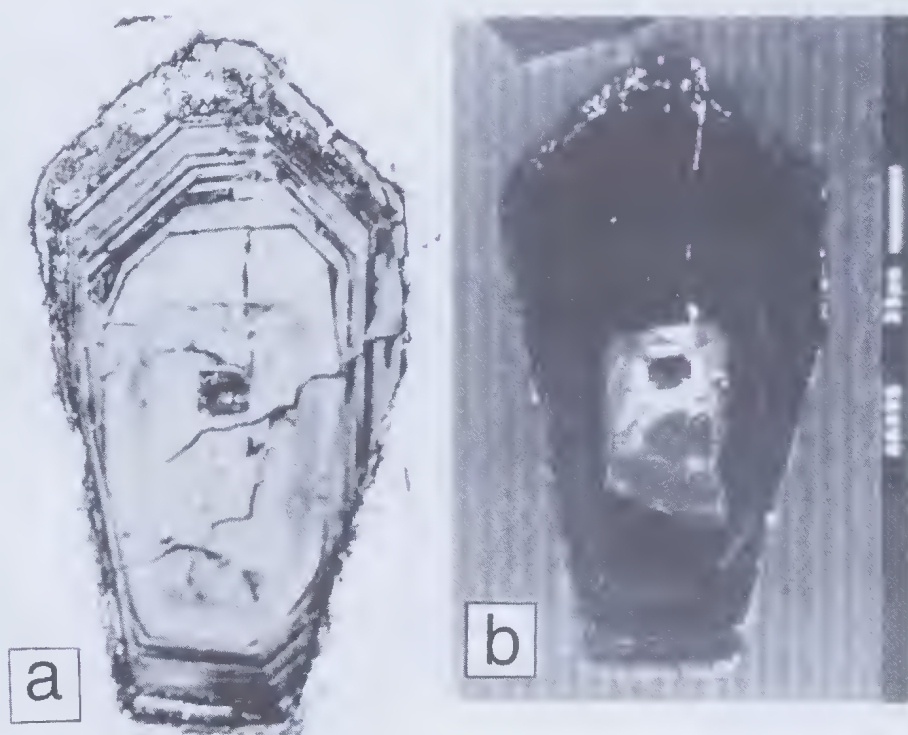


Figure 1. A cathodoluminescence (CL) image and a photomicrograph of the same polished zircon grain that has been subjected to HF etching. **A** CL of this grain is weak, although faint euhedral zoning can be seen in the rim and the rounded outline of a central core can be distinguished. An irregularly-zoned rectangular area defined by relatively strong luminescence is present in the core and may be an earlier zircon fragment. **B** The HF etched zircon also shows the outline of the central zircon core. The core itself is highly crystalline and unetched except for a weakly expressed irregular grey zone within the core at a position approximately marginal to the rectangular centre identified by strong CL. This marginal zone does not appear to be recorded by the CL image. On the other hand the etched zircon shows no sign of the rectangular area in the core clearly defined by CL. HF etching shows the fine euhedral zoning of the zircon margin much more clearly than the CL image.

higher the number, the more electrons an area will “reflect” and the brighter it will appear (Hanchar & Miller 1993). Hence the images can be termed atomic number (Z) contrast images. BSE imaging is now used widely in a variety of geological studies and is recognised as a powerful tool for studying zonation in accessory minerals. (e.g. Paterson *et al.* 1992; Miller *et al.* 1992; Wayne *et al.* 1992). Hanchar & Miller (1993) consider that Hf is primarily responsible for the variability in BSE intensity, with U having a secondary effect. Both elements have a much higher atomic number than the principal constituents of zircon (Zr, O, Si), so their substitution results in increased brightness.

BSE and cathodoluminescence appear to be similar except that in general dark areas in CL are bright in BSE, and vice versa. However, in the light of explanations for these effects it is not evident that cathodoluminescence will always provide an identical image to BSE. This has yet to be investigated.

HF etching is another technique used to highlight the internal structures of zircons. This measures the reactivity of the zircon to HF vapour. Radiation damage disordering of the lattice appears to enhance reactivity to HF vapour but high concentrations of contaminant elements may also be a factor in increasing reactivity to HF. There is some suggestion that quartz can form through unmixing in some areas in a zircon lattice (Sommerauer 1976; McLaren *et al.* 1994) and this would certainly

enhance reactivity with HF. Highly crystalline zircon is very resistant to HF etching.

We have observed differences in the zircon images determined by CL and HF etching. The example in Figure 1 shows HF etching and CL imagery of a single zircon crystal from an Archaean granite from the Darling Range. The HF etching identifies an unetched central area surrounded by an inner rim of oscillatory zoned zircon and a thin outer rim of granular etched zircon. The CL image shows features in the central part of the zircon not identified by HF etching and also the margin of the central zircon core, but does not resolve the zoned structure in the outer zircon rims. These differences may reflect the sensitivity of the two techniques to differences in zircon crystallinity. So far the possibility that differences in the degree of metamictness of a zircon may influence the CL emission has not been investigated. To investigate this and other questions involving the effects of recrystallisation on SHRIMP results, it is necessary to be able to measure quantitatively the crystallinity of an area on a zircon crystal the size of a SHRIMP analysis spot.

Qualitative determination of the crystallinity of zircon on the scale of a SHRIMP spot

X-ray powder diffractometry is commonly used to measure the crystallinity or the degree of

metamictization in zircons. However, the amount of sample necessary for this method of analysis is much larger than the average mass of a single zircon grain. Thus, in most cases X-ray diffractometry gives only summary information about entire grains or populations of grains.

Important advances in understanding the nature of the metamict state and the relevance of this to the interpretation of zircon U-Pb ages have been made by McLaren *et al.* (1994) using high-resolution transmission electron microscopy (HRTEM) studies of zircon on the scale of the zircon lattice. HRTEM gives local information about the degree of crystallinity, but at present this technique needs specially prepared samples and cannot be used for the routine determination of the crystallinity of micro-areas on the scale of SHRIMP analytical spots.

Vibrational spectral analysis. Vibrational spectra techniques of infrared and Raman spectroscopy appear to have the greatest promise for investigating zircon structure quantitatively on a microscale.

Woodhead *et al.* (1991) report that the **Infrared spectra** of zircon vary as a function of metamictization. This is shown by increasing band widths and decreasing intensities with increasing U-Th content. This technique has also been used to investigate the presence of OH in the zircon lattice (Woodhead *et al.* 1991). These authors have applied the technique to single grains, but although McLaren *et al.* (1994) refer to measurements with this technique on a micro-scale, the author is not aware of applications on the scale of a SHRIMP analytical spot. On the other hand the ability of **Raman spectrometry** to quantitatively measure zircon crystallinity on this scale has been convincingly demonstrated (Nasdala *et al.* 1996; van Bronswijk & Pidgeon 1994). Modern Raman microprobes can determine the crystallinity of zircon with a lateral resolution of about one micron and a volume resolution of less than 5 μm^3 . This opens up new opportunities for correlating structural, chemical and isotopic data on the same micro area within a zircon grain. With decreasing crystallinity, the Raman bands become less intense, are increasingly broadened and show lowered frequencies. In particular the increasing width of the internal $\nu_3(\text{SiO}_4)$ vibration (asymmetric stretching of SiO_4 tetrahedra) is sensitive enough to give a precise measure of the increasing degree of metamictization.

Some questions

Numerous question have been raised by studying the complex internal structures of zircons with these techniques combined with SHRIMP measurements. Some of these are as follows.

Radiation damage ages versus SHRIMP ages. An investigation of the relationship between zircon crystallinity and structures revealed by cathodoluminescence has not been made, although Raman spectroscopy has confirmed the relative crystallinity of zircon areas shown by HF etching. With careful calibration, involving standard zircons, crystallinity measurements by Raman spectroscopy can be combined with U-Pb concentrations determined by SHRIMP, to calculate a radiation damage age for a SHRIMP analytical spot. In this way it would be possible to construct a radiation damage age map of the

zircon and investigate the recrystallisation history of the zircons and the relationship of recrystallisation to the distribution of U,Th,Hf and U-Pb ages.

Diffusion versus reaction in zircon crystals. Zircon is considered the most refractory of the geochronologically useful uranium bearing minerals and is known to survive anatexis, granitic magma emplacement and magmatic crystallisation without loss of radiogenic Pb. This, together with the sharpness of zonal boundaries in zircons as old as 3000Ma, suggests that diffusion in zircon is extremely slow. However there is now evidence from HF etching studies and Raman spectroscopy that suggests some igneous zircons have undergone recrystallisation, with accompanying loss of Pb and U, soon after crystallisation. This does not appear to be related to radiation damage but is thought to involve expulsion of contaminant elements during lattice recrystallisation.

The significance of low U,Th crystalline cores. The cores of many zircons consist of low U-Th crystalline zircon, very resistant to HF etching, but sometimes show structure revealed by CL (Figure 1). Cores can represent xenocrysts of much older source material and have older SHRIMP ages. In some cases apparent cores have ages close to the magmatic age. These may represent older source material that has been updated or reflect processes affecting early formed zircon in the magma. Cathodoluminescence combined with HF etching and Raman spectroscopy will play an important part in resolving this question.

Structural complexities in other minerals. Cathodoluminescence and etching techniques appear to be limited in investigating minerals other than zircon. However, back scattered electron imagery has successfully revealed complex structures in titanite (Paterson & Stephens 1992) and monazite (De Wolf *et al.* 1993) and it is likely that other minerals will also have complex structures which will be important in interpreting their U-Pb ages.

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A review of Pb-isotope constraints on the genesis of lode-gold deposits in the Yilgarn Craton, Western Australia

N J McNaughton & D I Groves

Key Centre for Strategic Mineral Deposits, Department of Geology and Geophysics,
The University of Western Australia, Nedlands WA 6907

Abstract

Archaean lode-gold deposits within the Yilgarn Craton of Western Australia have made a major contribution to world gold production over the last century. However, models for the genesis of this class of deposits, particularly aspects of fluid and solute sources, remain controversial and require specific tests of their veracity. A systematic study of the initial Pb-isotopic compositions of Yilgarn lode-gold deposits and potential source rocks for ore components places constraints on possible source regions, and hence genetic models of ore formation.

The inferred initial isotopic composition of Pb in Yilgarn ore deposits correlates with that of the crustal Pb in the rocks of hosting greenstone belts, but is independent of the host rock to the deposit. Accordingly, the ore-deposit initial Pb-isotope compositions show regional variations with crustal rocks. These are inferred to vary with the age, composition and degree of metamorphic-magmatic depletion of the lower to middle crust, which is considered to be the source of Pb in the deposits. With the available geological constraints, the heterogeneous source can be modelled as follows; derivation from early Archaean (≥ 3.7 Ga) crust which is metamorphically depleted and/or partially melted at *ca.* 3.3 Ga; further reworking from *ca.* 2.7 Ga; and then sampling of the Pb in this heterogeneous crust by auriferous fluids at *ca.* 2.63 Ga. The Pb isotope modelling of source regions is not unique, but requires that the ore deposit Pb has an older crustal component which varies systematically on a regional scale independent of the composition, metamorphic grade and age of crustal rocks. This constrains the source of Pb in lode-gold deposits to include a component from the high-grade mid- to lower-crust via either metamorphic or magmatic processes.

Introduction

Lode-gold deposits in the Yilgarn Craton account for much of the annual gold production in Australia (*i.e.* 175 tonnes Au in 1995). Understanding the mode of formation of such deposits is pivotal to discovering new unexposed deposits, and hence much effort has been directed towards the establishment of robust deposit models which are predictive. The isotopic composition of Pb in ore deposits may be used as a tracer of Pb sources, and hence help constrain mineralisation processes. To use Pb isotopes as a source tracer, it is important to determine; (i) the initial Pb-isotopic composition and age of the ore system, and (ii) the coeval Pb in potential sources in, or below, the terrain hosting the gold deposit.

Over the last decade, colleagues and students of the authors at the Key Centre for Strategic Mineral Deposits have utilised the joint mass spectrometer facilities at Curtin University as part of multidisciplinary research into lode-gold deposits. This contribution describes the role of Pb-isotope tracer studies in developing the current understanding of Archaean lode-gold deposit source-regions within the Yilgarn Craton of Western Australia.

Geological background

The Yilgarn Craton is composed of; (i) greenstone belts consisting of volcanic, sedimentary and intrusive

rocks, which are typically metamorphosed and variably deformed, and (ii) complex granitoid-gneiss terrains which separate the greenstone belts (Gee *et al.* 1981). Almost all of the Yilgarn lode-gold production comes from areas within greenstone belts.

Mineralisation may occur in various styles, from breccia lodes, vein sets, laminated veins or shear zones and as disseminated lodes. However, there are a number of common characteristics of lode-gold deposits (summarised by Groves 1993; Groves *et al.* 1995); an epigenetic timing of mineralisation, varying broadly from syn-metamorphic in deposits hosted by mid-amphibolite to granulite facies rocks, to post-metamorphic in deposits hosted by greenschist to low-amphibolite facies rocks, a ubiquitous structural control on mineralisation with deposits commonly forming adjacent to secondary or higher order splays off major faults or shear zones, a gold-only element association where base metal enrichments are generally negligible and K, LILE, CO₂, Na or Ca are added to proximal wallrocks, an H₂O $\pm$ CO₂ $\pm$ CH₄, low-salinity ore fluid, and a range of crustal depths, from near surface (very low metamorphic grade) environments to granulite facies conditions, for gold mineralisation.

Age of lode-gold mineralisation

For Pb isotope modelling purposes, it is important to constrain the age of lode-gold mineralisation. As predicted by the crustal continuum model, Archaean lode-gold deposits of the Yilgarn Craton are broadly coeval at

2.64–2.63 Ga (Groves 1993). Although the available reliable data are few, Pb–Pb and Sm–Nd isochrons, mineral U/Pb ages and Ar–Ar plateau ages for hydrothermal or alteration minerals associated with mineralisation are broadly synchronous (Clark *et al.* 1989; Barnicoat *et al.* 1991; Wang *et al.* 1993; Kent 1994; Kent & McDougall 1995), although at least one major deposit (Mt Charlotte) may be 30 m.y. younger than the nearby Golden Mile mineralisation (Kent & McDougall 1995). In addition, age constraints provided by the youngest granitoids cut by lode-gold deposits and dykes which cut mineralisation are in agreement with the direct dating of mineralisation (e.g. Kent 1994; Bloem *et al.* 1995; Kent & McDougall 1995). Hence, for the Pb isotope modelling presented below, an age of 2.63 Ga is taken for mineralisation. In addition to the dating of the lode-gold deposits, relative timing criteria and age estimates for metamorphic and deformational events (McNaughton *et al.* 1990a) are also compatible with this age. Magmatic activity broadly synchronous with mineralisation includes suites of late granitoids in the Murchison Province (Wiedenbeck & Watkins 1993; Yeats 1996), and a suite of late granites within the granitoid-gneiss terrains of the southwestern Southern Cross Province (Qiu *et al.* 1995).

Lead reservoirs coeval with lode-gold mineralisation

Unlike ore systems where the initial Pb-isotope compositions can often be determined from ore sulphides, it is more difficult to determine the coeval Pb-isotope composition of the rocks which may represent the reservoirs for Pb contributing to the ore fluid. The only common mineral which may allow initial Pb-isotope ratios to be estimated is K-feldspar, which is generally restricted to granitoids. Other minerals and rocks have $U/Pb > 0$ and hence their Pb-isotope ratios have changed since formation. However, these materials may be analysed, and knowing the age of mineralisation, allow constraints to be placed on their Pb-isotope ratios at the time of mineralisation.

Granitoids

Granitoids of the Norseman-Wiluna belt of the Eastern Goldfields Province of Western Australia have been analysed and data are shown in Figure 1. The estimated composition of crustal rocks within the belt at 2.63 Ga is based on the Pb in a synvolcanic VHMS deposit at Teutonic Bore, and granitoids at Stennet Rocks, both compositions recalculated from their formation age to 2.63 Ga (McNaughton *et al.* 1990a,b).

The initial Pb-isotope compositions of the granitoids, based on K-feldspar data, are divided into three groups (Fig 1). The main group shows all data constrained to within two 2.63 Ga isochrons shown as parallel lines, and with K-feldspar data concentrated towards the intersection of the crosscutting crustal line. This group includes all available data on granitoids which are intrusive into the greenstone belts north of the Victory mine, Kambalda. Towards the west and south of Kambalda, the granitoids fall above these parallel lines, whereas, towards the northeast and east in the Eastern Goldfields Province they fall below these lines (both open circles; Fig 1). For comparison, granitoid K-feldspar data from

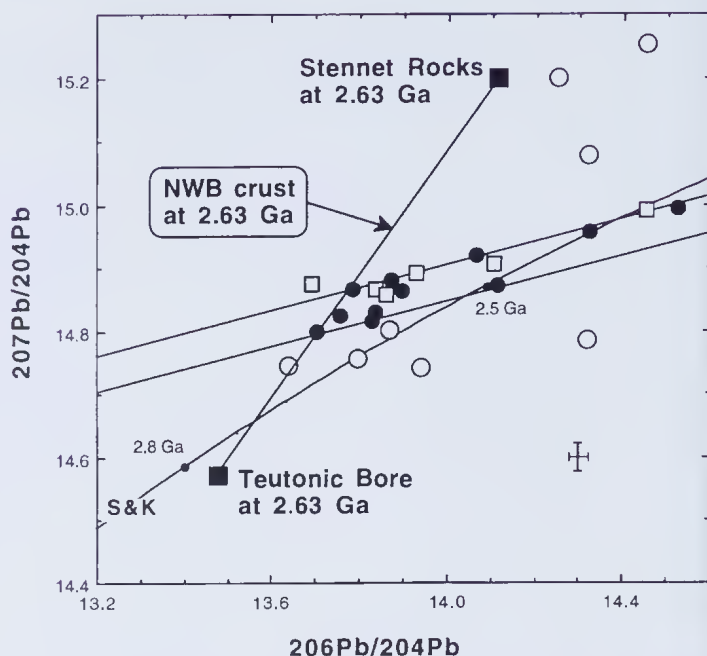


Figure 1. Common Pb-isotope plot showing K-feldspar data compared to the Stacey & Kramers (1975) lithospheric growth curve and the estimated composition of the crustal rocks of the Norseman-Wiluna belt (NWB) at the time of gold mineralisation (i.e. from Stennet Rocks to Teutonic Bore at 2.63 Ga; McNaughton *et al.* 1990b). Error bars are 2σ . Symbols; closed circles = NWB granitoids intrusive into greenstones north of Kambalda with 2.63 Ga isochrons bracketing these data; open circles (below parallel lines) = intrusive granitoids of the Northeastern Goldfields; open circles (above parallel lines) and Stennet Rocks = intrusive granitoids of the Norseman area and south of Coolgardie; open squares = Murchison and Southern Cross data. References; Oversby (1975). McNaughton & Bickle (1987), Perring & McNaughton (1992), Knight (1994). Wang *et al.* (1993), Ojala (1995), and unpublished data.

the Murchison and Southern Cross Provinces are also shown (open squares; Fig 1), and broadly overlap the granitoid trend in the Norseman-Wiluna belt.

The granitoids of the northeastern Eastern Goldfields Province are interpreted to have a different source region to all other areas. The inferred boundary of this isotopically distinctive terrane approximately corresponds to the position of the Keith-Kilkinny lineament. Towards the south and west of Kambalda, older crustal rocks in the granitoid source regions have been inferred on the basis of isotopic data (Oversby 1975; Perring & McNaughton 1992).

Greenstones

The Pb-isotope data for lithologies within greenstone belts in the Norseman-Wiluna belt are shown in Figure 2. Relative to the estimated crust at 2.63 Ga and the main granitoid field (shown as parallel lines; from Fig 1), the rocks of the Norseman region plot largely above the granitoid data, whereas those of the Kambalda-Kalgoorlie-Mt Pleasant region plot below. These data are modern Pb-isotopic compositions. The Pb in each rock at the time of mineralisation is not known, but will plot along a 2.63 Ga isochron fitted to each data point but at a less radiogenic composition. Scatter in the data may be induced by open system behaviour of Pb–U between volcanism and modern times, but the general adherence of data to consistent fields suggests this effect is minor.

Therefore, the initial Pb-isotope ratios for the greenstones could lie on the 2.63 Ga crustal mixing line, slightly above and below the granitoid data.

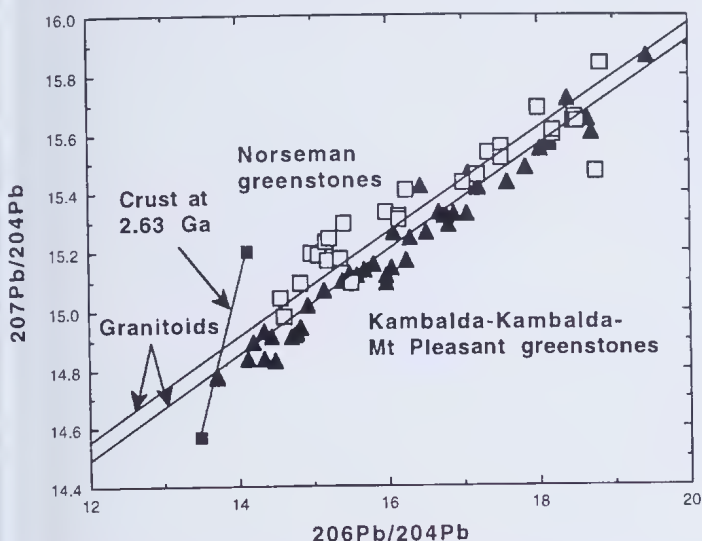


Figure 2. Common Pb-isotope plot showing the Norseman-Wiluna belt crustal mixing line and 2.63 Ga isochrons bracketing the granitoid Pb field (from Fig 1) compared to all greenstone data for the Kambalda-Kalgoorlie-Mt Pleasant region (triangles), and the Norseman region (squares). Data from: open squares (Perring & McNaughton 1992; McCuaig & McNaughton, unpublished data); closed triangles (Roddick 1983; Chauvel *et al.* 1985; McNaughton *et al.* 1988; Gebre-Mariam *et al.* 1993).

As with the granitoid data, the distinctly more radiogenic Pb in greenstones from the Norseman area, compared to the Kambalda-Kalgoorlie-Mt Pleasant area, represents a fundamental and provincial difference in the source of the Pb in both the greenstones and intrusive granitoids. The (gradational?) boundary between these different regions lies somewhere south of Kambalda and north of Norseman. Importantly, the southern part of the Norseman-Wiluna belt shows the most radiogenic Pb in both the granitoid and greenstone lithologies. To date, there are no published Pb-isotope data on greenstone lithologies from outside the Norseman-Wiluna belt.

Initial lead isotope composition of ore systems

The initial Pb of lode-gold ore systems is best determined from Pb-rich minerals genetically associated with the ore. Lead sulphide (galena) or tellurides are used, if they are present, but Fe-sulphides (pyrite, pyrrhotite) are more common and reliably preserve the initial Pb-isotope compositions in some cases (e.g. Ho *et al.* 1994). In a few cases, K-feldspar, sphalerite and scheelite associated with the ore have yielded reliable initial Pb-isotope ratios (Barnicoat *et al.* 1991; unpublished data).

Galena, with $\text{U}/\text{Pb} = 0$, is considered to be the best sampling medium to establish the initial Pb-isotope composition of lode-gold ore system. Galena occurs as a trace mineral in a proportion of lode-gold deposits. However, previous studies have shown that it does not always preserve the initial Pb of the ore system (e.g. Browning *et al.* 1983; Perring & McNaughton 1990; McNaughton *et al.* in

press). Similarly, Pb tellurides may be used (Browning *et al.* 1983), but are rarer than galena. Iron sulphides are common ore-related minerals in the majority of deposits, and, with proper sampling methodologies (e.g. Ho *et al.* 1994), can yield the initial Pb-isotope ratios. For most deposits, a number of ore sulphide samples have been analysed and an assessment of the data must be made to determine if the initial Pb ratios are preserved. In deposits where a range of Pb-isotope compositions occur, the least radiogenic composition is taken as the best estimate of the initial Pb (e.g. Ho *et al.* 1994). More radiogenic compositions are attributed to *in situ* U-decay, from U either within the sulphide or within inclusions in the sulphide, or from more radiogenic Pb mobilised into the sulphide from an external source after sulphide formation. In the following discussion, only initial Pb-isotope compositions, which are inferred using the criteria discussed above and by McNaughton *et al.* (1990b) and Ho *et al.* (1994), are considered.

Figure 3 presents the initial uraniumogenic Pb-isotope ratios of deposits within the Norseman-Wiluna belt. The data form a linear array, and show provinciality *i.e.* a systematic change in Pb-isotope composition between geographic regions (Groves *et al.* 1995). The least radiogenic end of the array is represented by deposits to the north of the belt, whereas the most radiogenic data are from around Norseman at the southern end of the belt. These differences correlate with both the granitoid (Fig 1) and greenstone data (Fig 2) from these regions. Further, within some areas along the regional strike of the greenstone belts, the initial Pb-isotope ratios from deposits are invariant at the scale of >100kms (e.g. Mt Pleasant area to Kalgoorlie to Victory mine, Kambalda; McNaughton *et al.* 1993), whereas other areas show systematic changes on this scale (e.g. from Victory mine, Kambalda to Norseman; Fig 3). There is a weak correlation

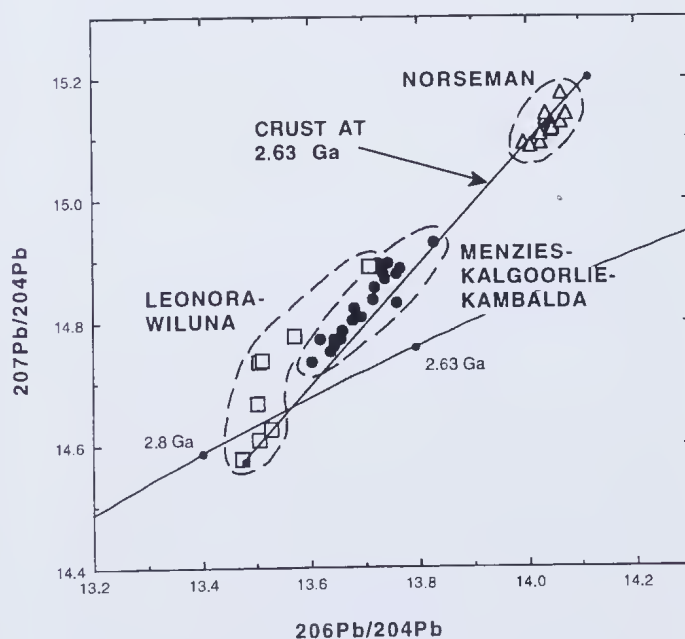


Figure 3. Common Pb-isotope plot showing the initial Pb for gold deposits from the Norseman-Wiluna belt, Stacey & Kramers (1975) growth curve and the crustal mixing line at 2.63 Ga from Fig 1. The gold deposit data fall into groups which correlate with geographical regions. Data from: McNaughton *et al.* (1990b, 1993) and Groves *et al.* (1995).

between initial Pb-isotope compositions of greenstone-hosted deposits and location across regional strike towards the granitoid-gneiss terrains (McNaughton *et al.* 1993). However, the initial Pb-isotope compositions for the deposits appears to be independent of hostrock (McNaughton *et al.* 1993; Ho *et al.* 1994).

The data for lode-gold deposits elsewhere in the Yilgarn craton are shown in Figure 4. There is a significant overlap with the Norseman-Wiluna belt data, although some deposits in the Murchison Province show significantly lower $^{206}\text{Pb}/^{204}\text{Pb}$ at similar $^{207}\text{Pb}/^{204}\text{Pb}$ (Fig 4). Griffin's Find in the Southern Cross Province is special in that the deposit occurs in the highest metamorphic grade setting of any deposit so far recognised (discussed below), and it is noteworthy that it has a similar initial Pb-isotope composition to other deposits (Fig 4).

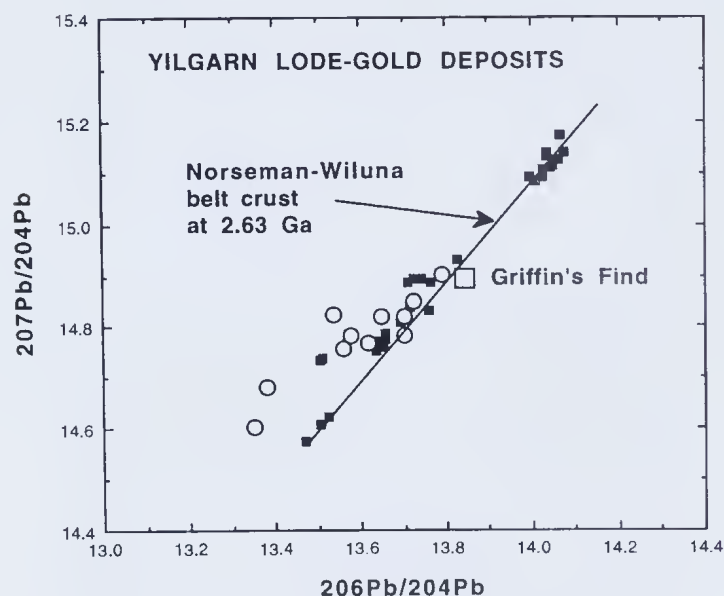


Figure 4. Common Pb-isotope plot showing the initial Pb for gold deposits from the Eastern Goldfields (closed squares), Murchison and Southern Cross Provinces (open circles, with Griffin's Find indicated), and the Norseman-Wiluna belt crustal mixing line at 2.63 Ga from Figure 1. Data from: McNaughton *et al.* (1990, 1993), Vielreicher *et al.* (1994) and Ojala (1995).

Discussion

Archaean Yilgarn Craton: Source of Pb in deposits of the Norseman-Wiluna belt

The initial Pb-isotope data from the lode-gold deposits of the Yilgarn craton (Fig 4) are compared with the estimated crustal Pb at the time of mineralisation in Figure 5. The ore deposit data for the Norseman-Wiluna belt correlate well with the 2.63 Ga crustal trend (Fig 3). As the crustal trend at 2.63 Ga is based on estimates of the Pb-isotope compositions of exposed upper crustal rocks, it could be inferred that the source of Pb in the deposits is also from the same upper crustal reservoir. However, the radiogenic endmember of the 2.63 Ga crustal trend is represented by a granitoid which undoubtedly attained its initial Pb from its lower to middle crustal source. Similarly, the lower granulite facies deposit at Griffin's Find in the Southern Cross Province (Barnicoat *et al.* 1991) also has an initial Pb-isotope composition close to this crustal trend (Fig 4), suggesting that both the upper and mid-

lower crust in the craton were broadly similar in their Pb-isotope characteristics at 2.63 Ga. Similarly, the overlap of Pb-isotope data from deposits from the Murchison, Southern Cross and Eastern Goldfields provinces (Fig 4) suggests that this heterogeneous upper-lower crustal source of Pb found in the gold deposits occurs on a regional scale, and that mineralisation was broadly coeval on this scale.

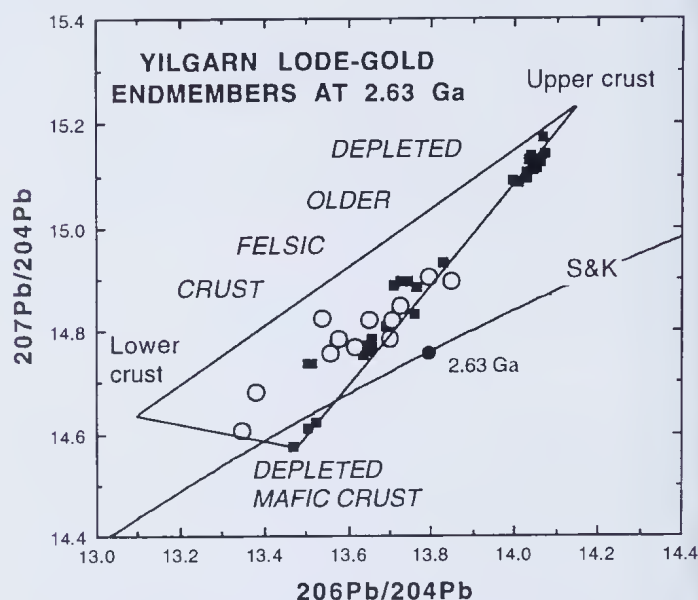


Figure 5. Common Pb-isotope plot showing the ore-deposit initial Pb-isotope compositions from Figure 4, and the inferred crustal endmembers (modified from McNaughton *et al.* 1990b).

The radiogenic nature of Pb from deposits, greenstones and granitoids of the Norseman region, compared to other regions, implies that all owe their Pb characteristics to a common source. Given that zircon xenocrysts and cores to *ca.* 2.7–2.63 Ga magmatic zircon grains within granitoids from this region and other parts of the Yilgarn have ages up to 3.5–3.3 Ga (Hill *et al.* 1989; Qiu *et al.* 1995), the preferred explanation of the Norseman radiogenic signatures is that they are due to older crustal rocks underlying this region (*cf.* Oversby 1975; Campbell & Hill, 1988). This radiogenic Pb signature can be modelled (see below) and must include a significant period of evolution, prior to 2.63 Ga, with enhanced U/Pb, typical of upper crustal rocks.

The least radiogenic endmember of the 2.63 Ga crustal trend, and overlapping data for lode-gold deposits (Fig 5), fall close to the global lithospheric growth curve of Stacey & Kramers (1975), but at model ages significantly older than the age of mineralisation (McNaughton *et al.* 1990a). Assuming that the lithospheric growth curve is valid, this implies that the Yilgarn craton has not evolved like typical Archaean crust (*e.g.* Richards 1983), and includes a stage of retarded Pb-isotope growth prior to 2.63 Ga. Modelling of potential sources to achieve the observed results yield an infinite number of solutions, and other geological constraints must be applied. The simplest model requires older felsic crust undergoing high grade metamorphism and depletion of U with respect to Pb, at least a few hundred million years prior to mineralisation. This process would produce the Teutonic Bore endmember Pb (of the crustal trend) at 2.63 Ga with

an older model Pb age (Fig 3). As the radiogenic endmember of the Norseman-Wiluna Belt 2.63 Ga crustal trend also requires an older crustal source, it follows that all the Pb from the 2.63 Ga crustal trend in Figure 5 requires an older crustal component at 2.63 Ga.

The greenstone data (Fig 2) do not show the large variation recorded in either the crustal trend or the ore deposit data. Assuming the outcropping greenstones are representative of greenstones at deeper levels, it follows that the greenstones cannot be the dominant source of Pb in the deposits. A deep source of Pb (*i.e.* below the greenstones) for the lode-gold ore deposits from underlying crust isotopically similar with the granitoids must be inferred at 2.63 Ga. A deep source of Pb in the deposits is also compatible with the observation that the initial Pb is independent of hostrock composition and crustal depth of mineralisation (*i.e.* depths corresponding to lower granulite to subgreenschist facies metamorphic conditions), as well as the epigenetic timing and ubiquitous relationship of deposits to splays of major faults and shear zones, which could allow ore fluids from deeper levels to access the entire crustal section.

Archaean Yilgarn Craton: Source of Pb in all deposits

The ore-deposit initial Pb data from the entire Yilgarn Craton are also shown in Figure 5 with estimated compositions of crustal reservoirs. The Pb mixing trend at 2.63 Ga for the crustal rocks of the Norseman-Wiluna belt in Figure 5 is interpreted to represent mid-lower to upper crustal Pb from older crust. The radiogenic endmember reflects a growth stage with enhanced U/Pb (*i.e.* enriched or upper crustal Pb), whereas the other end is from depleted or mid-lower crust with low U/Pb and retarded Pb-isotope growth.

Data falling significantly to the left of this trend in Figure 5 come from the northern Yilgarn Craton (*i.e.* north of Leonora in the Norseman-Wiluna Belt and the northern Murchison Province), and require an additional Pb component which has experienced retarded growth in $^{206}\text{Pb}/^{204}\text{Pb}$ with respect to $^{207}\text{Pb}/^{204}\text{Pb}$, compared to the other data. However, the timing of the inferred U-depletion event cannot be the same as that producing the Norseman-Wiluna belt crustal and deposit trend at 2.63 Ga. At the time of gold mineralisation, Figure 5 shows the trend for crust which is 3.3 Ga old and was variably depleted-enriched (*i.e.* lower and higher U/Pb, respectively) at *ca.* 3.3 Ga. This crustal array has been fitted to the upper end of the Norseman-Wiluna belt crustal array at 2.63 Ga to essentially define the second side of a triangle of Pb-isotope compositions which enclose all initial Pb-isotope compositions for the ore deposits in Figure 5. The slope of the upper side of the triangle is defined by the ages for t_1 and t_2 (*i.e.* 3.3 and 2.63 Ga, respectively; see McNaughton 1987).

To obtain crustal Pb-isotope compositions significantly above the lithospheric growth curve requires crust older than 3.3 Ga which evolves up to 3.3 Ga with an enhanced U/Pb (*i.e.* as upper crust). Modelling granitoid source regions suggests that this crust is at least 3.7 Ga old (Cassidy & McNaughton, *unpublished observations*). This is approximately the age of the oldest crustal segment known in the Yilgarn Craton (Kinny *et al.* 1990), and 3.7 Ga is used in the modelling (shown in Fig 6) as the age of the protocrust underlying the Yilgarn craton.

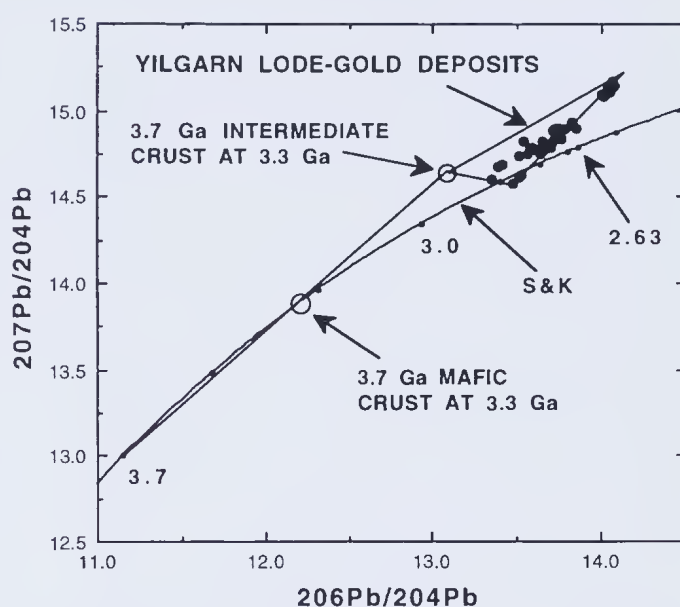


Figure 6. Common Pb-isotope plot showing the evolution of Pb from 3.7 Ga crust to produce the triangular field of crustal Pb-isotope compositions at 2.63 Ga, which encompasses the Yilgarn ore-deposit initial Pb-isotope compositions shown in Fig 5.

The triangular field for Pb-isotope compositions shown in Figure 5 can be modelled by forming a mafic-intermediate crust at *ca.* 3.7 Ga. The intermediate component is interpreted to have evolved with an average U/Pb higher than the Stacey & Kramers (1975) growth curve, whereas the mafic components remained near the lithospheric growth curves (*i.e.* U/Pb near the average lithosphere) until about 3.3 Ga, at which time the 3.7 Ga crust was variably depleted (*i.e.* metamorphosed-partially melted) in U with respect to Pb. On average, the mafic components are interpreted to have experienced an overall lowering of U/Pb, leading to retarded Pb-isotope growth from 3.3 Ga until 2.63 Ga, and produced compositions near, but slightly below, the growth curve, and to the left of the Stacey & Kramers lithosphere at 2.63 Ga (Fig 6; represented by the Teutonic Bore data in Fig 3). The 3.7 Ga old crustal components of intermediate composition must have evolved well above the Stacey & Kramers growth curve by 3.3 Ga (Fig 6), and were then variably depleted during the 3.3 Ga event, producing the upper side of the inferred triangular field in Figures 5 and 6 by 2.63 Ga. The average U/Pb of the intermediate crust must have been lowered to less than that of the mafic crust during the 3.3 Ga event, probably due to the preferential partial melting of the intermediate crust. This is interpreted to have produced very retarded Pb-isotope growth of the intermediate crust between 3.3 and 2.63 Ga.

The modelling described above allows for timing constraints of known and inferred formation ages of Yilgarn rocks and events. However, in detail, the modelled U/Pb for the post-3.3 Ga crust is unusually low, and the U/Pb of the 3.7 Ga intermediate crust prior to 3.3 Ga is unusually high. Both these anomalies would be lessened if the initial crust was older than 3.7 Ga, and/or the major depletion event was older than 3.3 Ga. The inferred *ca.* 4.2 Ga felsic crustal rocks of the northwestern Yilgarn (Kinny *et al.* 1990), and the presence of 3.3-3.5 Ga zircon xenocrysts in granitoids, indicate that such alternative models are feasible.

Conclusions

Lead isotope data from Yilgarn lode-gold deposits and presently exposed rocks may place important constraints on the crustal evolution and metallogenesis of the craton. Modelling of Pb-isotope compositions of rocks and ores within the known and partly inferred temporal framework of the craton can yield an infinite number of solutions. The Pb-isotope modelling suggested in this review (Fig 6) suggests that the Yilgarn craton is underlain by crustal rocks which may be >3.7 Ga old. This old crust comprised both mafic and intermediate components which evolved to form heterogeneous crust by the time of a major depletion event (metamorphism-partial melting) at ca. 3.3 Ga or older. Thereafter, the depleted crust evolved to produce Pb-isotope compositions at 2.63 Ga, the time of broadly coeval gold mineralisation across the craton, which lie within a triangular field of Pb-isotope compositions on a $^{207}\text{Pb}/^{204}\text{Pb}$ vs $^{206}\text{Pb}/^{204}\text{Pb}$ diagram, defined by crustal components with different geochemical compositions and histories. The initial Pb-isotope compositions of the gold deposits closely adhere to this triangular field, and, together with geological constraints, are best interpreted to indicate that all deposits obtained their Pb mostly from the older depleted crust at mid to lower crustal levels. This conclusion is compatible with a crustal continuum of deposits (Groves 1993) from granulite to subgreenschist facies settings, a ubiquitous spatial association with major crustal-scale shear or fault zones, the occurrence of deposits in all rock types and a similarity of geochemical and ore fluid characteristics on a craton scale (Ho *et al.* 1992; McNaughton *et al.* 1992, 1993). The deep source of Pb constrains the fluid source to high metamorphic grade regions, and implies that mineralisation resulted from either high grade metamorphic or deep magmatic processes.

Acknowledgements: This summary reflects a decade of research by many past and former members of the Key Centre for Strategic Mineral Deposits and its precursors; all are thanked. Special thanks go to M Dahl for technical assistance, the Curtin University mass spectrometrists, particularly W Chisolm, I Fletcher and K Rosman, continued funding from UWA, Curtin and ARC, and finally, and most importantly, to John de Laeter whose foresight and energies were instrumental in establishing the world-class mass spectrometry facilities in Western Australia.

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Isotopic constraints on the age and early differentiation of the Earth

M T McCulloch

Research School of Earth Sciences, Australian National University, Canberra 0200

Abstract

The Earth's age and early differentiation history are re-evaluated using updated isotopic constraints. From the most primitive terrestrial Pb isotopic compositions found at Isua Greenland, and the Pilbara of Western Australia, combined with precise geochronology of these localities, an age 4.49 ± 0.02 Ga is obtained. This is interpreted as the mean age of core formation as U/Pb is fractionated due to sequestering of Pb into the Earth's core. The long-lived Rb-Sr isotopic system provides constraints on the time interval for the accretion of the Earth as Rb underwent significant depletion by volatile loss during accretion of the Earth or its precursor planetesimals. A primitive measured $^{87}\text{Sr}/^{86}\text{Sr}$ initial ratio of 0.700502 ± 10 has been obtained for an early Archean (3.46 Ga) barite from the Pilbara Block of Western Australia. Using conservative models for the evolution of Rb/Sr in the early Archean mantle allows an estimate to be placed on the Earth's initial Sr ratio at ≈ 4.50 Ga, of 0.69940 ± 10 . This is significantly higher than that measured for the Moon (0.69900 ± 2) or in the achondrite, Angra dos Reis (0.69894 ± 2) and for a Rb/Sr ratio of $\approx 1/2$ of chondrites corresponds to a mean age for accretion of the Earth of 4.48 ± 0.04 Ga.

The now extinct ^{146}Sm - ^{142}Nd ($T_{1/2}^{146} = 103 \times 10^6$ yrs) combined with the long-lived ^{147}Sm - ^{143}Nd isotopic systematics can also be used to provide limits on the time of early differentiation of the Earth. High precision analyses of the oldest (3.8-3.9 Ga) Archean gneisses from Greenland (Amitsoq and Akilia gneisses), and Canada (Acasta gneiss) do not show measurable ($> \pm 10$ ppm) variations of ^{142}Nd , in contrast to the 33 ppm ^{142}Nd excess reported for an Archean sample. The general lack of ^{142}Nd variations, combined with the presence of highly positive ϵ_{143} values ($+4.0$) at 3.9 Ga, indicates that the record of large-scale Sm/Nd fractionation events was not preserved in the early-Earth from 4.56 Ga to ≈ 4.3 Ga. This is consistent with large-scale planetary re-homogenisation during ongoing accretion of the Earth. The lack of isotopic anomalies in short-lived decay systems, together with the Pb and Sr isotopic constraints is thus consistent with core formation and accretion of the Earth occurring over an ≈ 100 Ma interval following the formation of meteorites at 4.56 Ga.

Introduction

A fundamental question concerning the origin of the Earth is its age. Did the Earth accrete shortly after the formation of primitive meteorites at 4.56 Ga or was there a substantial interval before final accretion and early differentiation of the Earth? Conclusive answers to this question remain elusive, but a number of lines of evidence that are considered here now appear to indicate that the accretion of the Earth was not completed until at least 100 Ma after the formation of chondrites. The difficulty in establishing a precise age for the Earth arises from the lack of a geological record of the first ≈ 500 Ma of Earth history. The only known remnants from this period are 4.27 Ga detrital zircons found in an Archean sediment from the Jack Hills region of Western Australia (Compston & Pidgeon 1986). This provides a firm minimum age for the Earth, but the question of what happened between 4.27 Ga and 4.56 Ga remains. Insights into the Earth's earliest history can however be obtained from both the long-lived Rb-Sr, Sm-Nd and U-Pb systems as well as the now extinct ^{146}Sm - ^{142}Nd decay series.

The formation of the Earth by accretion of planetesimals was undoubtedly a complex process involving large-scale melting, internal differentiation of a metallic core and formation of a crust. These processes were characterised by distinctive patterns of geochemical fractionation, and it is this time, or mean age of parent/daughter fractionation which is registered by isotope systems. In the case of the U-Pb system, Pb has as a strongly chalcophile character and as a result was probably strongly partitioned into the Earth's core. Thus the substantially higher ($\approx 100\times$) U/Pb ratio for the Earth's mantle relative to carbonaceous chondrites is attributed to Pb being sequestered into the Earth's core along with sulphur. For this reason, the U-Pb system provides constraints on the average time of formation of the Earth's core. For the Rb-Sr system, the major cause of fractionation is the volatile nature of Rb compared to Sr. Thus the $\approx 10\times$ depletion of Rb in the Earth compared to chondrites is attributed to volatile loss processes during accretion of the Earth. In contrast to these systems, Sm and Nd are refractory elements, and are strongly fractionated only during magmatic differentiation processes. The question of the 'age of the Earth' is therefore be considered from a number of different aspects; the time-scales for accretion, core formation and early mantle differentiation.

Pb isotopic constraints on core formation

The application of long-lived radiometric chronometers to the question of the Earth's age was pioneered by Rutherford (1929). Based on the present-day abundances of the long-lived isotopes of uranium ^{235}U and ^{238}U , he deduced an approximate estimate for the timing of stellar nucleosynthesis and hence a maximum age of the Earth's of ≈ 4 billion years. The first precise estimate of the Earth's age was made by Patterson (1956) who showed that the Pb isotopic evolution of the Earth and meteorites approximately corresponds to a single-stage evolution from about 4.55 Ga to the present. This conclusion was based on the close proximity of the average modern terrestrial Pb to a 4.55 Ga isochron defined by meteorites. The value of modern terrestrial Pb used by Patterson was derived from the average Pb isotopic composition of marine sediments in the Pacific ocean. Since this pioneering work, it has now become apparent that modern rocks have a much more diverse range of Pb isotopic compositions indicative of complex, multi-stage evolutionary histories. For example, Allegre *et al.* (1995) has shown that modern mid-ocean ridge basalts (MORB's) have a wide range of generally younger single-stage Pb-Pb ages of from 4.3 Ga to 4.6 Ga.

In order to critically address the question of whether the Earth is significantly younger than its meteorite parent bodies, it is useful to consider the initial Pb isotopic composition of the oldest terrestrial rocks. Primitive terrestrial Pb compositions provide the least equivocal record of U-Th-Pb fractionation following the Earth's formation and hence the most reliable isotopic constraints on the Earth's age and early differentiation history. For a single-stage model of Pb evolution, the relationship between the parent ^{238}U and ^{235}U and daughter ^{206}Pb and ^{207}Pb isotopes is given by;

$$\frac{{}^{207}\text{Pb}/{}^{204}\text{Pb}(t) - {}^{207}\text{Pb}/{}^{204}\text{Pb}(I)}{{}^{206}\text{Pb}/{}^{204}\text{Pb}(t) - {}^{206}\text{Pb}/{}^{204}\text{Pb}(I)} = \frac{{}^{235}\text{U}(e^{\lambda' T_{\text{core}}} - e^{\lambda' t})}{{}^{238}\text{U}(e^{\lambda T_{\text{core}}} - e^{\lambda t})} \quad (1)$$

where ${}^{207}\text{Pb}/{}^{204}\text{Pb}(I)$ and ${}^{206}\text{Pb}/{}^{204}\text{Pb}(I)$ are the initial Pb compositions at the time of core formation T_{core} . ${}^{207}\text{Pb}/{}^{204}\text{Pb}(t)$ and ${}^{206}\text{Pb}/{}^{204}\text{Pb}(t)$ are the initial Pb compositions in early Archean rocks of age t (Table 1). The decay

constants for ^{238}U and ^{235}U are $\lambda = 0.155125 \text{ } \text{\AA}^{-1}$ and $\lambda' = 0.98485 \text{ } \text{\AA}^{-1}$ respectively, with ${}^{235}\text{U}/{}^{238}\text{U} = 1/137.88$. This equation enables the age of the Earth's core to be calculated using estimates of the Earth's initial Pb composition derived from meteorites, together with the most primitive Pb compositions preserved in ancient terrestrial rocks. Listed in Table 1 are samples with primitive Pb isotopic compositions; ie ${}^{206}\text{Pb}/{}^{204}\text{Pb} < 12$. An equally important constraint in the application of this equation is uncertainties in age of the early Archean initial Pb's (e.g. Gancarz & Wasserburg 1977). SHRIMP U-Pb dating of zircons has recently been undertaken at both Isua (Nutman *et al.* 1995) and in the Pilbara, for the Duffer dacite (McNaughton *et al.* 1993), the host of the Big Stubby galena. This improved chronology is particularly helpful in the interpretation of initial Pb's from the Isua supracrustal belt (Appel *et al.* 1978, Richards & Appel 1987). Nutman *et al.* (1995) have shown that this complex includes at least two felsic volcanic complexes with ages of $3.708 \pm 0.003 \text{ Ga}$ and $3.807 \pm 0.002 \text{ Ga}$, with the galenas listed in Table 1 being associated with the older volcanics of the western section.

Following the approach of Gancarz & Wasserburg (1977), the initial Pb's listed Table 1, are presented, using plots of ${}^{207}\text{Pb}/{}^{206}\text{Pb}$ versus ${}^{204}\text{Pb}/{}^{206}\text{Pb}$ (Fig 1). This diagram emphasises the evolution of Pb in the early Archean. It is apparent from Figure 1b that plausible ranges for ${}^{238}\text{U}/{}^{204}\text{Pb}$ (μ) of from 8.5 to 9.5, are required to be consistent with the evolution of Isua, Big Stubby as well as younger conformable Pb's (Stacey & Kramers 1974). With this range of μ the Pb-Pb age of the Earth's core, T_{core} is estimated to be from 4.52 Ga to 4.46 Ga (Table 1). This age is clearly younger than that of chondritic meteorites (4.563 Ga), and hence the value of initial Pb given by Canyon Diablo (Tatsumoto *et al.* 1973) must be adjusted to take into account the Pb evolution from the time of meteorite formation, at 4.563 Ga to $\approx 4.50 \text{ Ga}$. The average μ for carbonaceous chondrites is low (< 0.2) and based on the correlation of Pb/U versus K/U, a $\mu_1 \approx 1$ is inferred (Allegre *et al.* 1995) for the proto-Earth prior to core formation. Thus the corrected initial Pb for the Earth at $\approx 4.50 \text{ Ga}$ is given by;

$${}^{206}\text{Pb}/{}^{204}\text{Pb}(I) = {}^{206}\text{Pb}/{}^{204}\text{Pb}(\text{CD}) + \mu_1(e^{\lambda 4.56} - e^{\lambda T_{\text{core}}}) \quad (2)$$

Table 1
Most primitive terrestrial Pb isotopic compositions and the age of the Earth's core

Locality	Age (Ma)	${}^{206}\text{Pb}/{}^{204}\text{Pb}$	${}^{207}\text{Pb}/{}^{204}\text{Pb}$	${}^{208}\text{Pb}/{}^{204}\text{Pb}$	T_{core} (Ga)	μ_2
ISUA						
261619 ^a	3807 ± 2	11.176	13.047	31.130	4.492	9.11
263654 ^a	3807 ± 2	11.311	13.147	31.267	4.419	11.0
2966 ^b	3808 ± 2	11.146	13.025	31.148	4.510	8.72
Amitsoq ^c	3590 ± 50	11.468	13.203	31.365	4.462	8.46
PILBARA						
Big Stubby ^{d,e}	3465 ± 3	11.912	13.707	31.838	4.495	8.71
Canyon Diablo	4563 ^f	9.307	10.294	29.476		
INITIAL Earth Pb						
	4490 ^g	9.330	10.339	29.495	$\mu_1 = 1.0$	

^a Richards & Appel (1987); ^b Appel *et al.* (1978); ^c Gancarz & Wasserburg (1977); ^d Richards (1986); ^e Pidgeon (1978); ^f Tatsumoto *et al.* (1973); ^g this study.

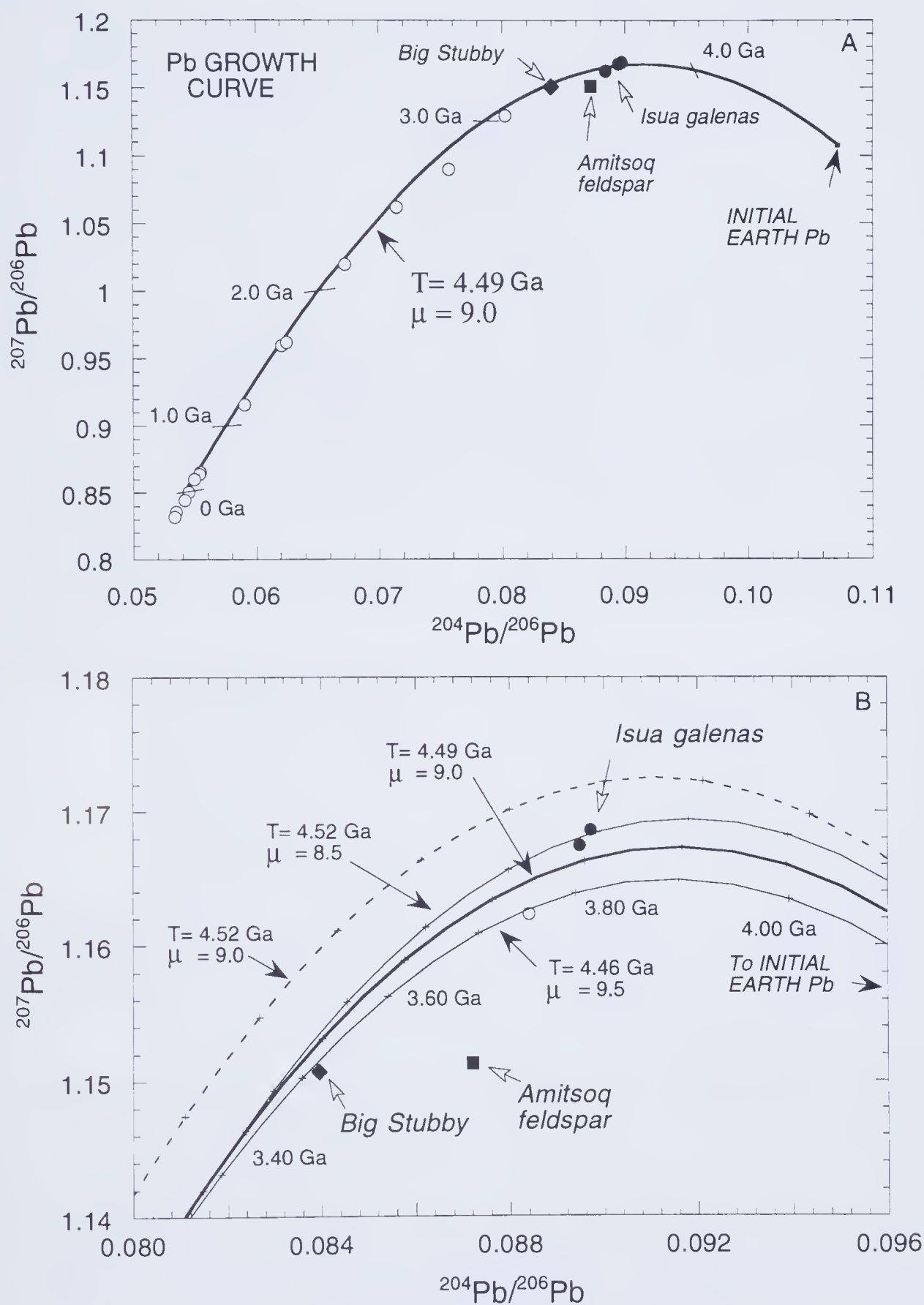


Figure 1A. Pb growth curve plotted using $^{207}\text{Pb}/^{206}\text{Pb}$ versus $^{204}\text{Pb}/^{206}\text{Pb}$. Primitive terrestrial Pb's are shown with solid symbols and open circles are galena Pb's tabulated by Stacey & Kramers (1974). Earth initial Pb from Canyon Diablo (Tatsumoto *et al.* 1973). B. Plot of the most primitive terrestrial Pb ($^{207}\text{Pb}/^{206}\text{Pb} < 12$) for galena from Isua, West Greenland (Appell *et al.* 1978; Richards & Appel 1987) and Big Stubby, Pilbara (Pidgeon 1978; Richards 1986). Amitsoq feldspar from Gancarz & Wasserburg (1977). Open circle shows disturbed younger sample from Isua (Richards & Appel 1987). The curves show the Pb evolution for $\mu = 8.5, 9.0$ and 9.5 . The best fit to both the Isua and Big Stubby Pb's is given for an age of the Earth's core of $T_{\text{core}} = 4.49 \text{ Ga}$ and $u_2 = 9.0$. Initial Earth Pb is evolved Canyon Diablo using $\mu_1 = 1$ from 4.56 Ga to 4.49 Ga .

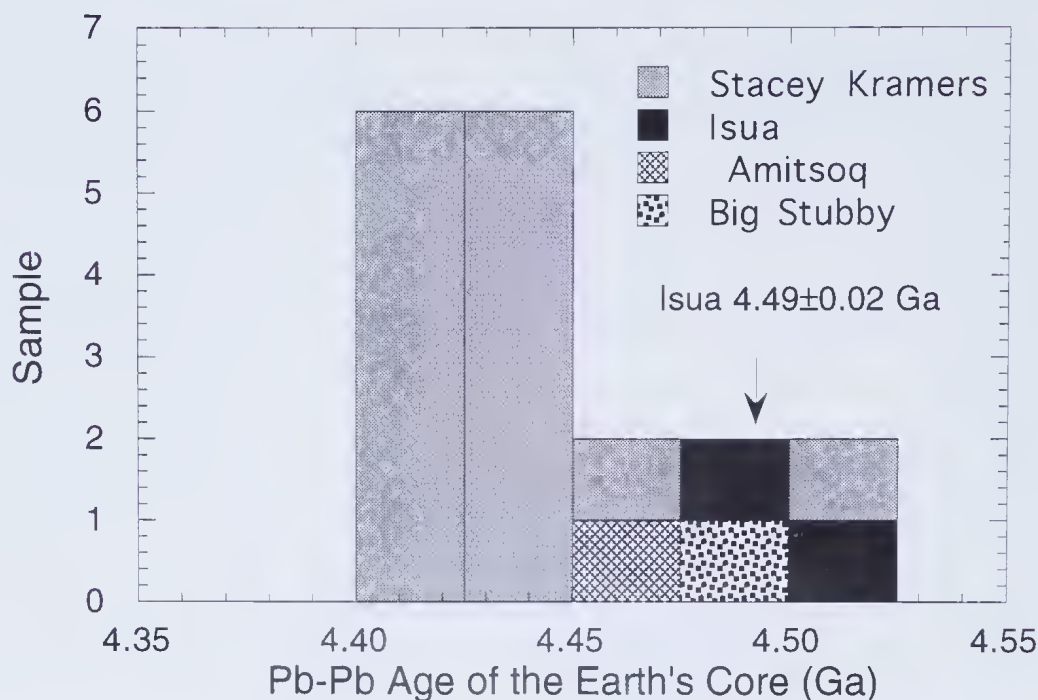


Figure 2. Histogram of single-stage Pb-Pb ages for the Earth's core calculated using data points shown in Fig 1. Arrow shows the best estimate for the mean age of formation of the Earth's core based on Pb-Pb ages from Isua and Big Stubby.

and an equivalent equation for $^{207}\text{Pb}/^{204}\text{Pb}(1)$. With this minor correction to the Earth's initial Pb and with $\mu_1 = 1$, (the μ from 4.56 Ga to 4.50 Ga) the best estimate of the age of the Earth's core using equation 1, is $T_{\text{core}} = 4.49 \pm 0.02$ Ga. This latter estimate is based on both the Isua as well as Big Stubby initial Pb's and is consistent with $\mu_2 = 9$ (the μ from 4.49 Ga to the present). It is noted that the initial Pb from the Amitsoq feldspar is not compatible with this data set, which may be due to the effects of metamorphic disturbance as discussed by Gancarz & Wasserburg (1977) and/or uncertainties in the crystallisation age of the Amitsoq feldspar sample.

Using the same approach, T_{core} ages have also been calculated for the set of younger conformable galena Pb's listed by Stacey & Kramers (1974). A histogram of T_{core} ages is shown in Figure 2 with ages of from 4.40 Ga to 4.50 Ga; these ages are somewhat younger than those from Isua and Big Stubby. Taken at face value, they are indicative of a longer interval (100-200 Ma) for core formation, however the younger galena have significantly more evolved Pb compositions and therefore their interpretation is more problematic.

Sr isotopic constraints on timescales for the accretion of the Earth

Based on the same reasoning as outlined for Pb, the most rigorous constraints on the Earth's initial Sr are those derived from the most primitive terrestrial Sr isotopic compositions. With this in mind, McCulloch (1994) reported a measured $^{87}\text{Sr}/^{86}\text{Sr}$ initial ratio of 0.700502 ± 9 for the 3.46 Ga barite from the North Pole dome of Western Australia. This result, together with a less precise initial Sr ratio for a basaltic komatiite from the Onverwacht Group (Jahn & Shih 1974), indicates an

initial Sr isotopic composition for the early Archean (3.46 Ga) mantle of 0.70050 ± 2 . This determination currently represents the most reliable value for the early Archean mantle and has important ramifications for the origin of the Earth-Moon system as well as the evolution of the Archean mantle. The key question is how accurate and how representative is this value for the early Archean mantle? Barite is a useful recorder of $^{87}\text{Sr}/^{86}\text{Sr}$ ratios, but due to its hydrothermal origin may provide only an upper limit to the Sr composition of the Earth's mantle, although in the early Archean the difference in Sr isotopic composition between seawater and the upper mantle is probably insignificant (McCulloch 1994). The consistency of the Pilbara barite result with the few available reliable determinations of initial Sr in the Archean mantle (Jahn & Shih 1974; Machado *et al.* 1986) together with the presence of primitive Pb in the nearby Big Stubby galena (Pidgeon 1978; Richards 1986) indicates that this is a plausible result.

The Earth's initial Sr ratio (BEBI = Bulk Earth Best Initial) can be calculated from the early Archean barite using the following single-stage model:

$$\text{BEBI} = (^{87}\text{Sr}/^{86}\text{Sr})_{\text{barite}} - (^{87}\text{Rb}/^{86}\text{Sr})_{\text{EARTH}} (e^{\lambda T_{\text{acc}}} - e^{\lambda t}) \quad (3)$$

where $T_{\text{acc}} = 4.50$ Ga is the mean age for accretion of the Earth, $t = 3.46$ Ga, the age of the Pilbara barite (McNaughton *et al.* 1993), $\lambda = 0.0142 \text{ \AA}^{-1}$ and $(^{87}\text{Rb}/^{86}\text{Sr})_{\text{EARTH}}$ the ratio from T_{acc} to t . Using a value for $(^{87}\text{Rb}/^{86}\text{Sr})_{\text{EARTH}}$ of 0.07 ± 0.007 (McCulloch 1994), which reflects the partially depleted character of the early Archean mantle, equation 3 gives a well defined value of $\text{BEBI} = 0.69940 \pm 10$. This estimate is significantly greater than that previously assumed using the initial Sr composition of achondrites (e.g. Angra dos Reis (ADOR) with $^{87}\text{Sr}/^{86}\text{Sr} = 0.69893 \pm 2$). Moreover, BEBI is significantly greater than the initial Sr ratio for the Moon (Nyquist *et al.*

1973; Alibert *et al.* 1994) of $LUN = 0.69900 \pm 2$ and thus allows chronological constraints to be placed on the first 100 Ma of evolution of the Earth-Moon system.

If we consider ADOR as a zero reference time-line for the accretion of planetary bodies, then the difference in the initial Sr compositions between ADOR & BEBI can be translated into a formation interval for planetary accretion relative to ADOR using;

$$I_{Sr}(BEBI) - I_{Sr}(ADOR) = \lambda \Delta T (^{87}\text{Rb}/^{86}\text{Sr})_p \quad (4)$$

where ΔT is the formation interval and $(^{87}\text{Rb}/^{86}\text{Sr})_p$ the parent/daughter ratio in the planetary precursor bodies. By far the most significant uncertainty in applying the ΔT - I_{Sr} methodology to planetary accretion is in estimating the $(^{87}\text{Rb}/^{86}\text{Sr})_p$ ratio of the terrestrial planetesimals. The use of a chondritic Rb/Sr ratio cannot be justified as the volatile/refractory ratio of the asteroid belt, as sampled by meteorites, is probably not representative of the solar nebular from which the terrestrial planetesimals accumulated (Taylor & Norman 1990). The ratio of volatile/involatile elements would be expected to increase radially outwards from the Sun following the T-Tauri stage, implying a lower $(^{87}\text{Rb}/^{86}\text{Sr})_p$ for proto-Earth materials than for chondrites. Unfortunately, the volatile/involatile ratio of the terrestrial planetesimals cannot be directly ascertained as these bodies were presumably swept up and accreted into the Earth-Moon system.

The other factor that needs to be considered is the extent of volatile loss during planetary formation, particularly if this occurs via accretion of only a relatively small number of more massive bodies with large gravitational potential's and consequently high accretional energies. Rb is volatile under reducing conditions at temperatures $<1000^\circ\text{C}$ whereas it is likely that the Earth's outer surface reached temperatures of $>1500^\circ\text{C}$ (Stevenson 1987). With reasonably efficient mixing of the upper portion of the Earth, concomitant with impact-accretion, it is highly likely that a significant fraction of the proto-Earth's volatile budget including Rb (and Pb) would not have been accreted. The actual magnitude of the Rb/Sr (*i.e.* volatile/refractory) fractionation that occurred during accretion of the Earth although obviously significant, is difficult to quantify. An upper limit to the extent of fractionation is given by the difference between the bulk Earth and chondritic $^{87}\text{Rb}/^{86}\text{Sr}$ ratios of 0.082 and ≈ 0.8 respectively. This indicates a maximum possible fractionation of Rb/Sr resulting from a combination of both planetary accretion and Solar nebular processes of $\approx 10\times$. An intermediate estimate is given by $(^{87}\text{Rb}/^{86}\text{Sr})_p = 0.4$ which implies a depletion of Rb/Sr in the terrestrial region of the solar nebular of $\approx 2\times$ compared to chondrites. For BEBI = 0.69940, this corresponds to ΔT of ≈ 80 Ma relative to ADOR (Fig 3). Substantially greater depletion in the volatile content of the terrestrial plan-

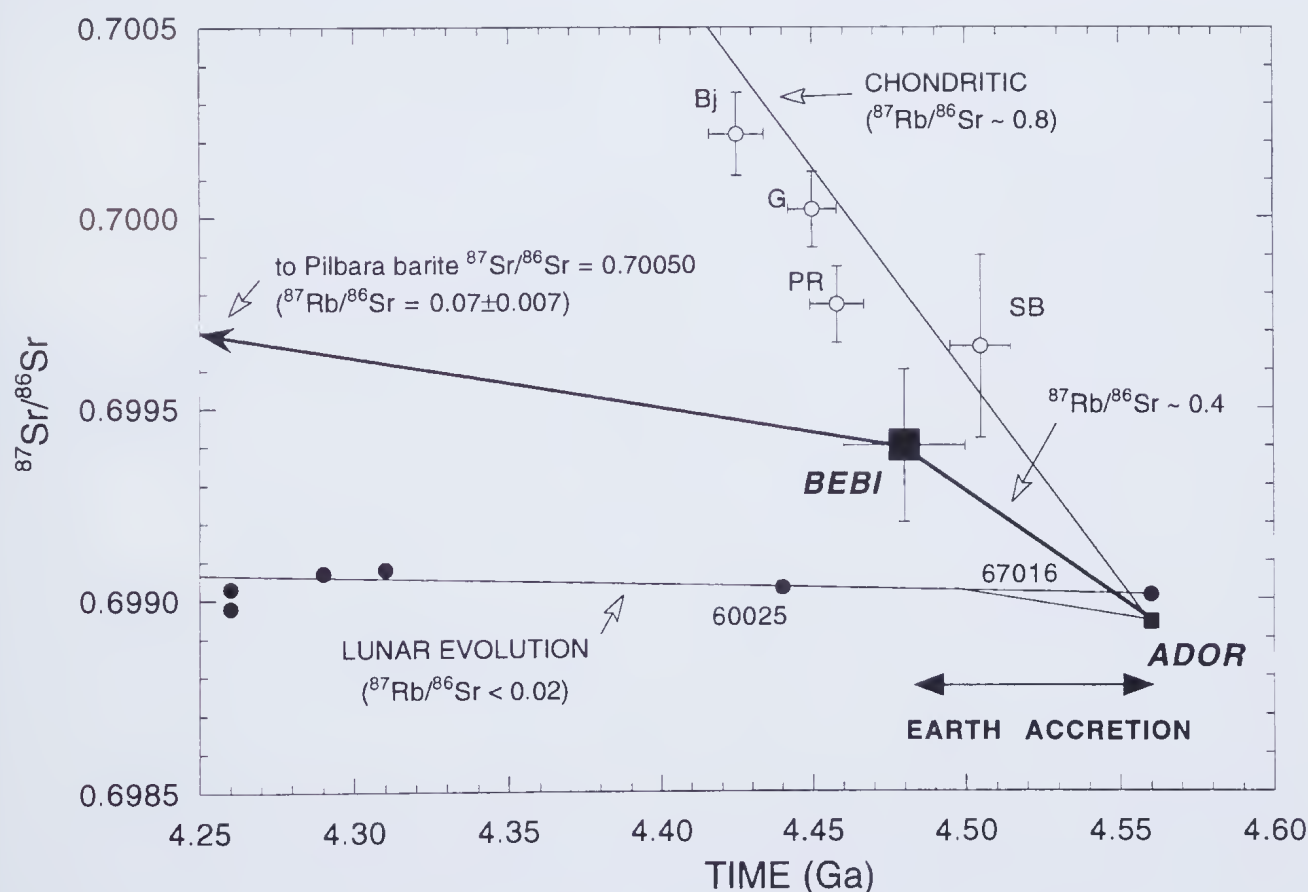


Figure 3. Plot of initial Sr composition versus time for the Earth = BEBI (McCulloch 1994), Moon shown with solid circles (Alibert *et al.* 1994) and ordinary chondrites with open symbols (Brannon *et al.* 1987), relative to the primitive differentiated achondrite Angra dos Reis = ADOR (Lugmair & Galer 1992; McCulloch 1994). Bj = Bjurbole, G = Guarena, PR = Peace River, SB = Soko Banja, (Brannon *et al.* 1987). The mean age for accretion of the Earth ranges from ≈ 80 Ma to 100 Ma for a $^{87}\text{Rb}/^{86}\text{Sr}$ ratio of ≈ 0.4 , which assumes an $\approx 50\%$ loss of volatiles during accretion.

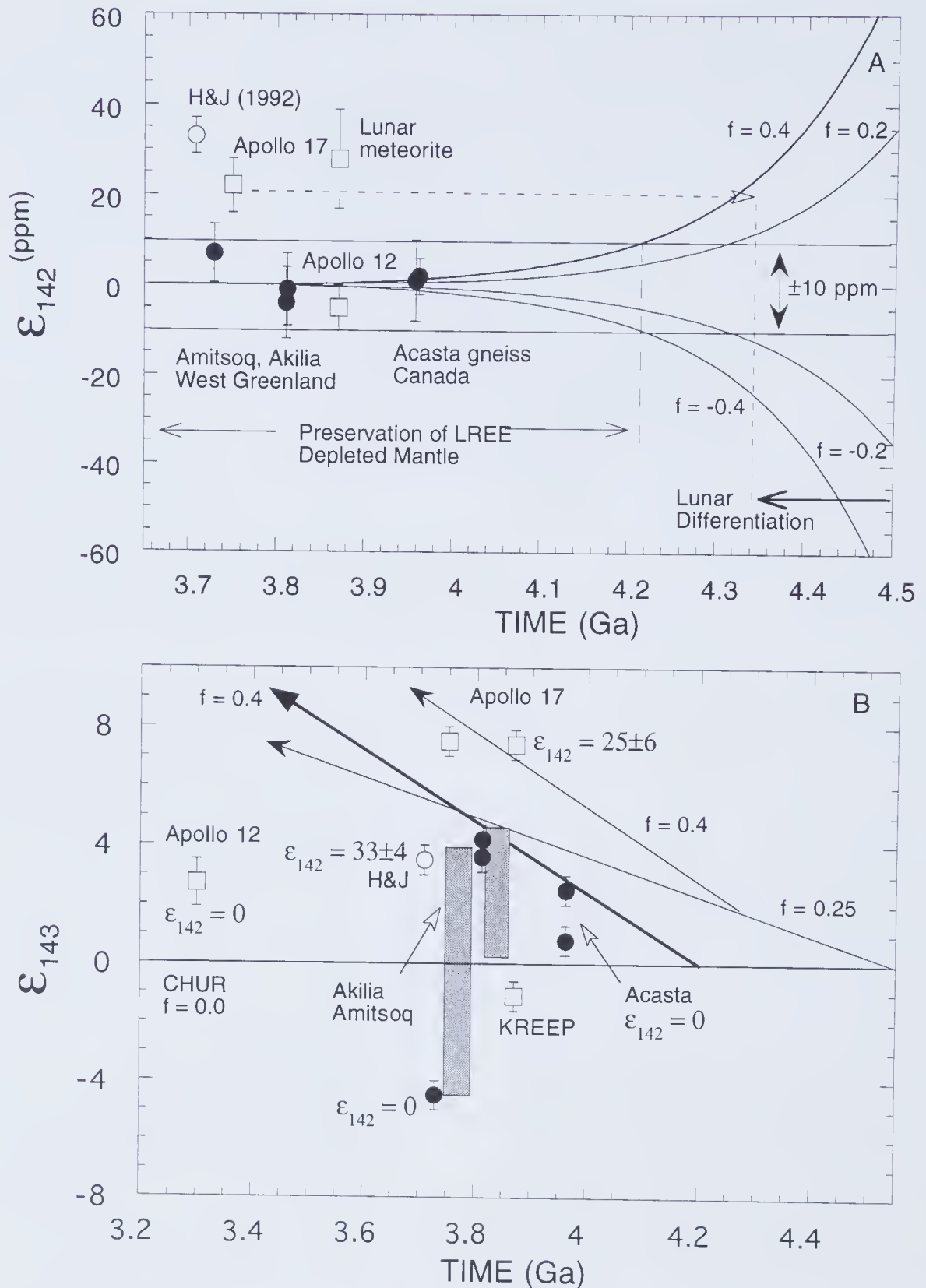


Figure 4A. Plot of ϵ_{142} versus time for an initial $^{147}\text{Sm}/^{144}\text{Sm} = 0.007$ (Prinzhofer *et al.* 1992). If a LREE depleted mantle ($f > 0.2$) formed in the first 200-300 Ma of Earth history then within the analytical resolution of ± 10 ppm it would be expected to preserve positive ϵ_{142} values. The general absence of terrestrial ϵ_{142} excesses (McCulloch & Bennett 1993) therefore suggests that fractionated terrestrial reservoirs were not preserved until after ≈ 4.3 Ga, after which, ^{147}Sm was extinct. Only a single positive ϵ_{142} value of 33 ± 4 ppm, has so far been reported by Harper & Jacobsen (1992). Lunar data is from Nyquist *et al.* (1995). B. Plot of ϵ_{143} versus time for earliest Archean rocks from Greenland (Amitsoq and Akilia are shaded regions) and Acasta gneiss from Canada (Bennett *et al.* 1993). Despite the large range of both positive and negative terrestrial ϵ_{143} values, there is general absence of associated terrestrial ϵ_{142} effects (samples shown in solid symbols) apart from that reported by Harper & Jacobsen (1993). This indicates that the terrestrial record of highly fractionated mantle reservoirs was not generally preserved until after ≈ 4.3 Ga. The Apollo 17 samples (Nyquist *et al.* 1995) with very positive ϵ_{143} values show relatively small ϵ_{142} effects of 25 ± 6 ppm (Fig 4A), consistent with crystallisation of the lunar magma ocean at ≈ 4.3 Ga.

etals is probably unlikely, as this would give $\Delta T > 100$ Ma, which would correspond to an age for the Earth that is younger than that obtained for terrestrial core formation (≈ 4.49 Ga) using Pb-Pb isotope systematics outlined previously.

Sm-Nd constraints on the Earth's age and early differentiation

In contrast to the U-Pb and Rb-Sr systems, the rare earth elements Sm and Nd are refractory elements that are strongly fractionated only during magmatic differentiation processes. The Sm-Nd isotopic system is however unique in having both extinct and "live" parent-daughter decay systems; the now extinct ^{146}Sm - ^{142}Nd with a half-life of 1.03×10^6 yrs, and the commonly used long-lived ^{147}Sm - ^{143}Nd system with a half-life of 1.06×10^{11} yrs. Owing to its short half-life, ^{146}Sm effectively became extinct at ≈ 4.30 Ga, at which time the $^{142}\text{Nd}/^{144}\text{Nd}$ ratio became essentially invariant. Positive or negative deviations in the observed $^{142}\text{Nd}/^{144}\text{Nd}$ ratio must therefore represent the effects of differentiation processes operative prior to 4.30 Ga. Thus ^{142}Nd isotopic abundances have the potential to reveal events occurring in the first 250 million years of the Earth history.

The combined ^{142}Nd - ^{143}Nd isotopic systematics can potentially provide constraints on the magnitude and the longevity of chemical differentiation in the early Earth due, for example, to the presence of an early magma ocean. Positive or negative deviations of ϵ_{142} values from the bulk Earth value are possible if a REE fractionated reservoir was formed within the first 100 to 200 Ma of Earth history and if this reservoir survived intact as a closed system until it could be sampled via magmatic processes and preserved in the oldest terrestrial rocks (3.70 - 3.96 Ga). This scenario is shown in Figure 4A where ϵ_{142} values are plotted versus the time of reservoir fractionation and isolation. In these calculations, it is assumed that the Solar System had $^{146}\text{Sm}/^{144}\text{Sm} = 0.007$ at 4.56 Ga, the same Sm isotopic composition as that determined from meteorites (Prinzhofer *et al.* 1992; Nyquist *et al.* 1995). The magnitude of any ϵ_{142} anomaly is directly dependent on the fractionation (f) where $f = [(\text{Sm}/\text{Nd}) / (\text{Sm}/\text{Nd})_{\text{CHUR}} - 1]$, as well as the time T when the reservoir fractionated and became isolated. Following Harper & Jacobsen (1992), the ϵ_{142} effects can be calculated from the following relationship;

$$\epsilon_{142}(t) = f Q_{142} [^{146}\text{Sm}/^{144}\text{Sm}] [e^{-\lambda_{146}(T_0-T)} - e^{-\lambda_{146}(T_0-t)}] \quad (5)$$

where $Q_{142} = 354 \text{ Ga}^{-1}$, $T_0 = 4.56 \text{ Ga}$, T = time of mantle differentiation, and t = crystallisation age of the rock.

Apollo 17 lunar basalts (Nyquist *et al.* 1995) show small ϵ_{142} effects of ≈ 25 ppm (Fig 4) together with very positive ϵ_{143} values of $> +7$ at 3.9 Ga (Fig 4B). This is consistent with crystallisation of the lunar magma ocean at ≈ 4.3 Ga with f values of from 0.25 to 0.4 (Fig 4B). The terrestrial samples analysed by McCulloch & Bennett (1993) are consistent with the lunar results of Nyquist *et al.* (1995), having ϵ_{143} values $\approx 1/2$ that of the Moon and no measurable ϵ_{142} effects > 10 ppm. Harper & Jacobsen (1992) have however reported an ϵ_{142} of 33 ppm value for a metasedimentary sample from Isua, with $\epsilon_{143} = 3.5$, the

latter being significantly smaller value than that found in Apollo 17 basalts. Thus at this time, the Harper & Jacobsen (1992) result must be considered anomalous with respect to both the Earth and Moon and not representative of the terrestrial early Archean mantle.

The strongly positive ϵ_{143} values shown in Figure 4B for terrestrial samples together with the lack of ϵ_{142} effects (McCulloch & Bennett 1993) provides a firm upper limit to the time of differentiation of the terrestrial mantle. These constraints require that highly fractionated LREE depleted reservoirs were formed and only preserved sometime after 4.3 Ga, by which time decay of ^{146}Sm was essentially complete. In the interval from ≈ 4.5 Ga, to 4.3 Ga the Earth's mantle was probably well mixed and constantly being rehomogenised, possibly due to the effects of giant impacts. The Nd isotopic results are therefore consistent with a relatively extended interval (≈ 100 Ma) for the formation of the Earth.

Discussion and Conclusions

The interpretation of ΔT 's determined using the Pb-Pb and Rb-Sr chronologies is not straightforward. Essentially, the Pb-Pb system records the integrated history of core formation while Rb-Sr records the volatile/refractory fractionation with neither system discriminating between various rates of core formation or accretion. Thus the ΔT inferred for the Earth of ≈ 100 Ma does not necessarily imply that the Earth accreted continuously throughout this interval. For example, the Earth may have formed essentially catastrophically in a period of $< 10^7$ yrs, but ≈ 80 to 100 Ma following the differentiation of ADOR. Alternatively, if accretion and core formation had been essentially continuous throughout this period, then the formation interval would have been significantly longer than the mean ages given by the Pb-Pb and Rb-Sr isotopic systems. In the latter case, the mean age for accretion and core formation of ≈ 4.49 Ga, implies a formation interval of ≈ 140 Ma (Fig 5). Thus a formation interval for the Earth of ≈ 100 Ma is a relatively conservative lower estimate.

What are the implications of a relatively prolonged formation interval for the Earth on the origin of the Moon? Assuming that the Earth and Moon were derived from similar precursor materials, then to account for the Moon's lower initial Sr ratio (Alibert *et al.* 1994), it is required to have formed first, probably via a giant impact on the proto-Earth, within ≈ 20 Ma of ADOR. The strong terrestrial geochemical signature of the Moon (Ringwood 1986) would have been inherited from the proto-Earth at this time, indicating that the Earth's core had started to form. Immediately following the giant impact, both the proto-Earth and proto-Moon are molten, but if large-scale differentiation occurs on the Earth, its effects were shortlived due to ongoing accretion and thorough mixing. From ≈ 4.54 Ga to ≈ 4.48 Ga, the Earth was rehomogenised while continuing to accrete the remaining $\approx 30\%$ of its final mass. Core formation probably occurred concomitantly with accretion rather than being triggered by a late-stage giant impact. Both the terrestrial Sr, Nd and Pb-Pb isotopic systematics are thus consistent with an extended (≈ 100 Ma) interval for the accretion of the Earth.

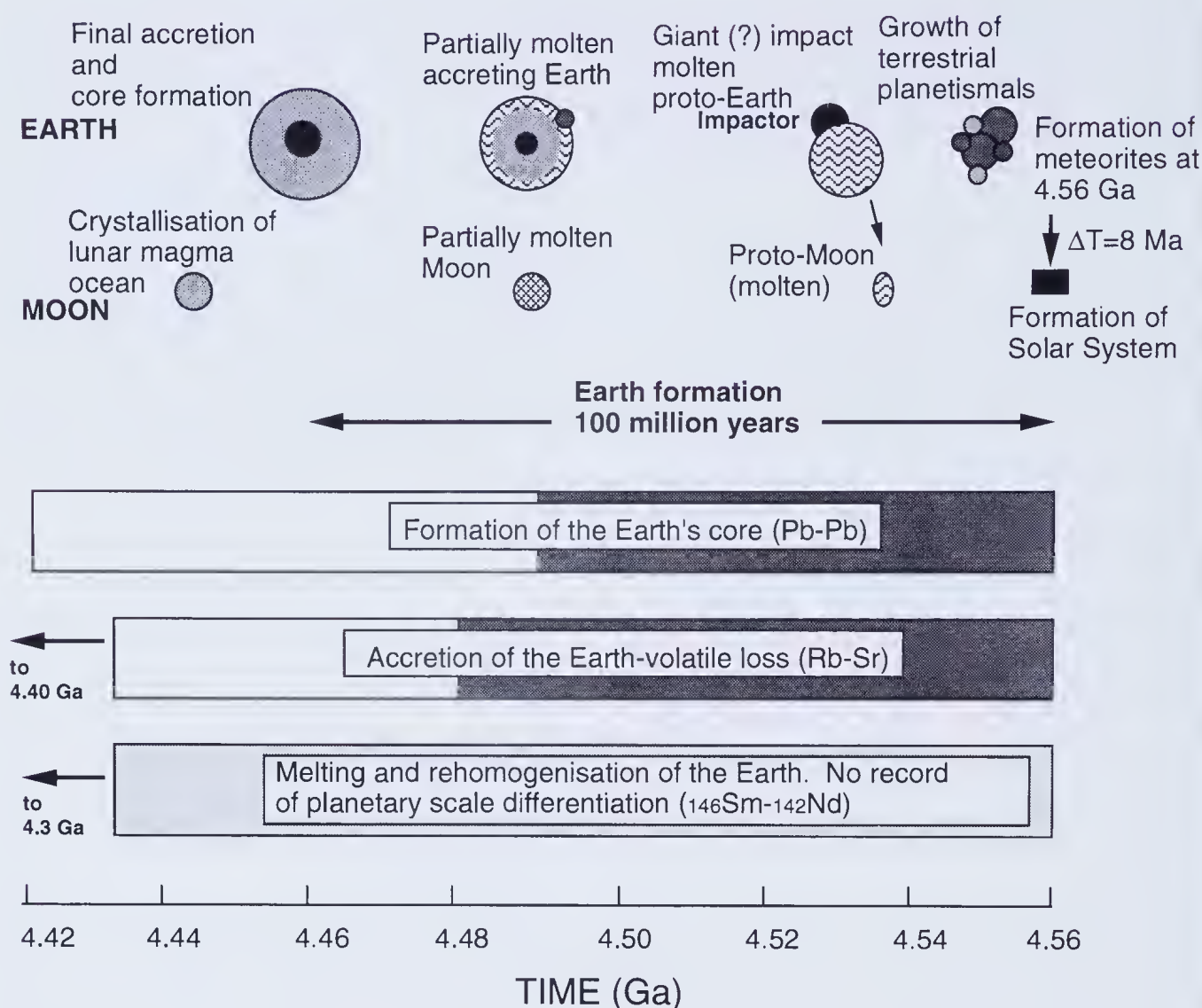


Figure 5. Schematic diagram illustrating the sequence of events during accretion and early differentiation of the Earth-Moon system. Meteorites first formed at 4.563 Ga with an ≈ 8 Ma range of ages (Allegre *et al.* 1995). The mean age for core formation and accretion of the Earth is 4.49 ± 0.02 Ga and 4.48 ± 0.04 Ga respectively (solid shading). Accretion and core formation may have continued until ≈ 4.42 Ga (open boxes) consistent with the Earth forming over at least an ≈ 100 Ma interval. Constraints from ϵ_{142} - ϵ_{143} values indicate that the differentiation of the mantle into distinctive long-lived reservoirs did not commence until after ≈ 4.3 Ga, consistent with rehomogenisation of the Earth's mantle during the first ≈ 200 -300 Ma of its history.

Acknowledgements: Professor John deLaeter's integrity, generosity and above all enthusiasm for doing science at the highest level has provided a superlative example for all his students to emulate. I'm indebted to John for my initiation into isotope geochemistry.

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A tale of two cratons: Speculations on the origin of continents

A F Trendall

Retired Director of Geological Survey of Western Australia 29 Troy Street, Applecross WA 6153

Abstract

The origin of continents is not well understood, perhaps because each of the two usual ways of addressing the problem has methodological difficulties. Isotope geochronology has enabled the condition of the early Earth to be reconstructed from the direct evidence of successively older rocks, working backwards in time. But, since a point is reached where there are no older rocks available, much speculation about the immediately pre-geological history of the Earth (the period when its identity was well established but of which no direct trace remains in the form of existing surface rocks) has come from planetology; and its approach has been, properly, to work forwards in time, starting from some preferred model of accretion. This paper is an attempt to bridge these two approaches, by focusing on what characteristics of the earliest rocks actually need to be explained by the planetological models.

The restriction of these oldest rocks to a small number of core areas within early cratons, of which the Kaapvaal Craton (KC) of southern Africa and the Pilbara Craton (PC) of Western Australia are taken as typical, is first noted. The closely parallel evolution of both of these Cratons starts at about the same time, with the sudden appearance of vast quantities of evolved silicic magma (now orthogneisses), accompanied by the deposition of thick successions of mixed, mainly volcanic, rocks differing in only a few respects from those that have continued to come from the Earth's interior; although the early Earth must have been hotter, this is not reflected in the metamorphism of the oldest strata. Following this abrupt beginning, these protocontinents grew steadily through continuous, but diminishing, magmatic activity, manifest as both silicic plutonism and bimodal eruption.

All of these features are consistent with the following simple model of the early Earth. A completely molten immediately pre-geological Earth had, outside its metallic core, a pattern of huge, polygonal, convection cells with ascending central plumes and descending peripheries; there were possibly as few as 12 such cells, forming a pattern of irregular pentagons, with 20 main centres of convective descent (COCDs) at their triple junctions. Before the continents formed, the thin skin of cooled and solidified material, formed on the surface of each cell during radial surface flow, was carried down at the margins and remelted as it descended. Such melting produced, by well known petrogenetic processes, a variety of differentiated magmas which during rapid early convection were carried down and remixed with their parent materials. As the whole Earth cooled, and the rate of convection slowed, a point was reached where the buoyancy of these silicic magmas enabled them to rise faster than the descending columns below the COCDs, resulting in the appearance at the surface of a plug of orthogneiss.

The subsequent geological development of the KC and PC, jointly taken as archetypes of the early continents, fits comfortably with a concept that later continental growth was a simple response to maintenance of the same large-scale convective system which remained in force long enough to establish, below the oldest parts of the continents, the very deep roots for which there is increasing evidence. At some stage of lateral growth, possibly associated with both a change of global convective patterns and the development of a layered mantle, the early continents became unstable and were subject to break-up and relative displacement over the Earth's surface. The existing areas of oldest rocks are not simply the few surviving remnants of some early (but not earliest) continental crust that covered the whole Earth, but really do represent both the initial and sole centres of continental growth.

Neutrinos: Ghosts of creation

J R de Laeter

Department of Applied Physics, Curtin University of Technology, Perth WA 6001

Abstract

The magnitude of the mass of an electron neutrino is still uncertain, yet this parameter is of vital importance to our understanding of cosmology, particle physics and neutrino oscillations. The process of double beta decay offers a means of testing grand unification theories as it may yield limits for the electron neutrino mass and indicate the degree of lepton conservation in elementary particle reactions. A number of measurements of the half-life of double beta decay of $^{130,128}\text{Te}/^{130,128}\text{Xe}$ and $^{82}\text{Se}/^{82}\text{Kr}$ have been obtained, but the values are almost certainly inaccurate because of leakage of the gaseous daughters over geological time. This may be overcome by measuring the double beta decay half-lives of nuclides which have solid daughter products. Improvements in solid source mass spectrometry now allow such measurements to be successfully attempted. The results of one such experiment will be described and other double beta decay systems which may yield experimental results suggested.

Introduction

On December 4th 1930, the Austrian physicist Wolfgang Pauli suggested that a particle might be responsible for carrying off the varying amounts of energy that seemed to be missing in beta decay. However, over two decades were to elapse before neutrinos were finally discovered by Reines & Cowan (1956). It has since been shown that there are different types of neutrinos - electron neutrinos which are emitted during beta decay, muon neutrinos which are associated with charged pion decay, and tau neutrinos.

The only way that neutrinos can interact with normal matter is through an extremely feeble force known as the weak interaction. Thus, in the "standard" model of particle physics, neutrinos are mass-less particles that do not disintegrate. There is some experimental evidence (albeit controversial) that neutrinos can oscillate from one form to another (Athanasopoulos *et al.* 1995). This can only occur if these neutrinos possess a mass. In 1987, supernova SN 1987A exploded in the Large Magellanic Cloud. From the spread in the arrival times of the burst of neutrinos emitted by SN 1987A, it could be calculated that the mass of the electron neutrino is less than 25eV.

One of the most successful developments of modern science has been the rapid evolution of nuclear astrophysics to what is now a mature scientific study. A study of nuclear astrophysics has enabled us to unravel many of the secrets of nucleosynthesis - those nuclear constraints which determine the abundances of the chemical elements. The isotope abundances of the elements, which we measure so precisely by mass spectrometry today, have been fashioned in the stars and interstellar medium over billions of years. Some are vestiges of the Big Bang itself.

The three basic processes involved in synthesising the heavy elements ($Z > 31$) are the slow (s) and rapid (r) neutron capture processes, and the proton (p) process, a reaction that synthesises the neutron-deficient isotopes. The s-process synthesises nuclides along the valley of nuclear stability during the red giant phase of a star's evolution, whilst the r and p processes occur on a much shorter time scale in cataclysmic, non-equilibrium environments, such as supernova. De Laeter (1990) has described these nucleosynthetic processes in greater detail.

Figure 1 shows a section of the Chart of the Nuclides in the vicinity of tin. The r-process nuclides mimic fission product decay chains and produce neutron-rich isotopes, in some cases far from the valley of stability. From the nuclear stability of these r-process even-even nuclides, it can be shown that they cannot be absolutely stable, yet the fact remains that they have sustained their existence in measurable quantities over geological time. There is therefore a need for a nuclear decay mechanism to exist that is sufficiently slow to enable these nuclides to survive in significant quantities over a period of many billion years.

Double beta decay is just such a mechanism in that its half-life is in excess of 10^{17} years (Mayer 1935). The nuclear systematics of double beta decay is applicable to even-even nuclides on the neutron-rich side of the valley of nuclear stability, thus enabling survival of these nuclides over geological time scales.

Double beta decay

Double beta decay is the rarest nuclear phenomenon in Nature. In double beta decay, a nucleus undergoes a transmutation from one element to another such that two electrons are emitted rather than the single electron emitted, in the more commonly observed single beta decay. All of the parent and daughter isotopes involved in double beta decay are even-even nuclei. The pairing force acting between like nucleons is responsible for the

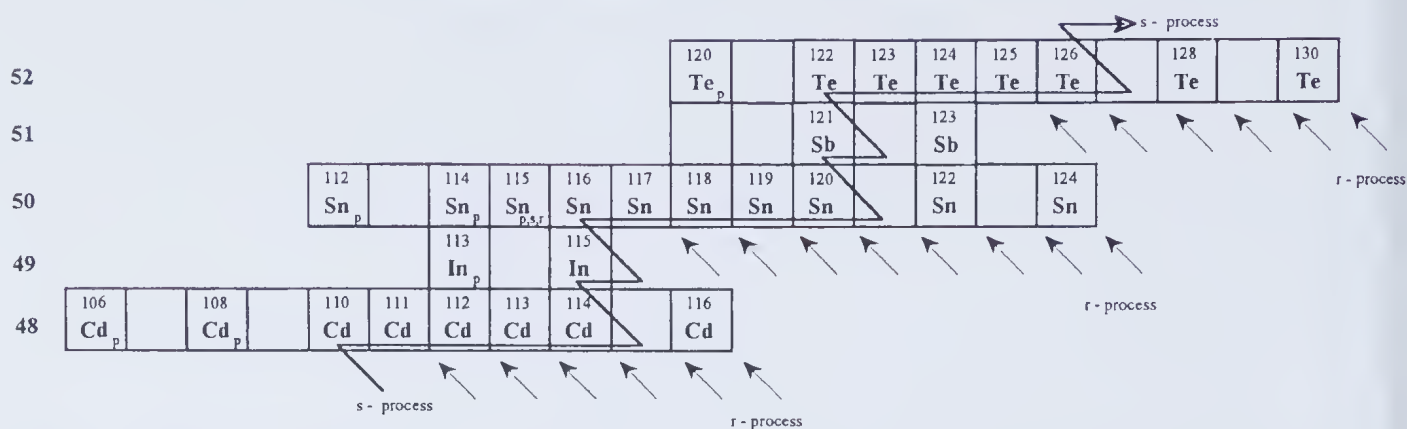


Figure 1. A section of the Chart of the Nuclides in the vicinity of tin. The arrows represent nuclides produced by the r-process, which indicates the various modes of nucleosynthesis.

increase in the binding energy of these nuclei relative to the odd-odd isotopes, thus preventing a single beta decay.

The long standing question in double beta decay is whether the electron neutrino should be described by a Dirac or by a Majorana field (Primakoff & Rosen 1981). In the Dirac formalism, the neutrino has a distinct anti-particle such that:

$$(A, Z) \rightarrow (A, Z + 2) + 2e^- + 2\bar{\nu}_e$$

However, if the neutrino is a Majorana particle then the neutrino and anti-neutrino are indistinguishable, so that double beta decay can occur with the net emission of no neutrinos such that;

$$(A, Z) \rightarrow (A, Z + 2) + 2e^-$$

Grand Unified Theories of particle physics allow the neutrino to have a finite mass, thus allowing the possibility of neutrino-less double beta decay. However, double beta decay systems have such long half lives (10^{17} - 10^{24} years; Doi *et al.* 1985), that enormous experimental constraints are imposed on the detection of double beta decay daughter products.

There are two approaches to measuring the half-life of a double beta decay reaction. In the direct detection method, coincidence counting is used to measure the radioactivity at the energy value predicted from precise atomic mass measurements (Dyck *et al.* 1990). The disadvantage of the radioactive counting method is that intrinsically faster radioactivities, such as those associated with uranium or thorium decay chains, produce significant backgrounds which may mask the beta decay product. Instrumental experiments are designed to detect the electrons as they are emitted and are thus capable of not only measuring the lifetime of the double beta decay, but also the electron energy spectrum. Doi *et al.* (1988) have summarised a number of experimental results for the half-life of double beta decay on ^{76}Ge , ^{82}Se , ^{100}Mo , ^{136}Xe and ^{150}Nd conducted by a number of research groups (Table 1). The half lives range from $>6 \times 10^{18}$ years to $>1.4 \times 10^{21}$ years.

One of these direct detection experiments was conducted by the University of California, Santa Barbara and Lawrence Berkeley Livermore, 600m underground with eight 0.9kg Ge detectors. The detectors are inside a cavity formed by 10 blocks of 15 cm thick sodium iodide crystals providing an active volume with a 30 keV threshold. The sodium iodide crystals are in turn inside

Table 1

The data of the half-lives of the neutrinoless double-beta decay with Majorana emission for various nuclei. (Doi 1988 and primary references therein).

	Experimental group	Half-life (yr)
^{76}Ge	Osaka	$>2 \times 10^{20}$
	Moscow (ITEP)	$>2 \times 10^{20}$
	Batelle-South Carolina	$6 (\pm 1) \times 10^{20}$
	Caltech-SIN-Neuchatel	$>12 \times 10^{20}$
	Santa Barbara-LBL	$>14 \times 10^{20}$
^{82}Se	Irvine	$>4.4 \times 10^{20}$
^{100}Mo	Osaka	$>6 \times 10^{18}$
	Irvine	$>7.5 \times 10^{18}$
^{136}Xe	Milano	$>1.6 \times 10^{19}$
	Moscow (INR)	$>1.0 \times 10^{20}$
^{150}Nd	Moscow (INR)	$>7.0 \times 10^{19}$

a pure Pb shield of 20 cm thickness. The detectors are kept at liquid-nitrogen temperatures under vacuum. The detectors are tuned to search for electrons emitted from the $^{76}\text{Ge} \rightarrow ^{76}\text{Se}$ double beta decay with a 2.041 MeV summed electron energy, which is the total kinetic energy available for this particular reaction.

The second approach to measuring the half-life of a double beta decay reaction is based on the cumulative effects of double beta decay over geological time. This geochemical method depends on the mass spectrometric determination of the stable double beta decay product that has accumulated in geologically old minerals. The geochemical method does not directly determine the decay mode as is possible in the direct determination method. It indicates only the total decay probability of two neutrino decay $\lambda_{2\nu}$ and no neutrino decay $\lambda_{0\nu}$, $\lambda_{2\nu} + \lambda_{0\nu}$. However, for double beta decay accompanied by the emission of two neutrinos, the theoretically predicted decay probability $\lambda_{2\nu}$ is much smaller than that predicted in neutrinoless double beta decay $\lambda_{0\nu}$ by perhaps six orders of magnitude (Doi *et al.* 1985), although the actual value depends on the mass of the neutrino.

The geochemical method provides an upper limit to the double beta decay half-life because the gas retention age invariably post-dates the time of mineralisation; the direct detection method yields lower limits because of the possibility of background events. The direct detection

method has the potential advantage of being able to distinguish between the two double beta decay modes. In the case of the two neutrino double beta decay mode, the energy deposited in the detectors will show a continuous energy distribution up to the total transition energy, in the same manner as single beta decay. However, if neutrino-less double beta decay occurs, the sum of the energies of the two emitted electrons will be the total transition energy, and the energy spectrum will be a single narrow peak. The energy spectrum therefore provides a clear, unambiguous signature of the nature of double beta decay. The high resolution, double focusing mass spectrometer at the University of Manitoba has been used to determine double beta decay energy values for ^{128}Te and ^{130}Te of 867.2 ± 1.0 and 2528.8 ± 1.3 keV respectively (Dyck *et al.* 1990). The total kinetic energy available for any double beta decay system can be obtained from the atomic mass table of Wapstra & Audi (1985).

(1991) gives best estimates of these half-lives as 2×10^{24} y and 1×10^{20} y respectively. The results from these isotopic systems support the lepton-conserving, two neutrino mode of decay.

Table 2

Values reported for the half-life of ^{130}Te

Reference	Half-life
Inghram & Reynolds (1949)	1.4×10^{21}
Takaoka & Ogata, (1966)	8.2×10^{20}
Srinivasan <i>et al.</i> (1972)	2.5×10^{21}
Hennecke <i>et al.</i> (1975)	9.7×10^{20}
Kirsten (1983)	2.6×10^{21}
Richardson <i>et al.</i> (1986)	$< 1 \times 10^{21}$
Kirsten <i>et al.</i> (1986)	1.6×10^{21}
Manuel (1986)	7×10^{20}
Chiou & Manuel (1988)	7×10^{20}
Current best estimate	8×10^{20}

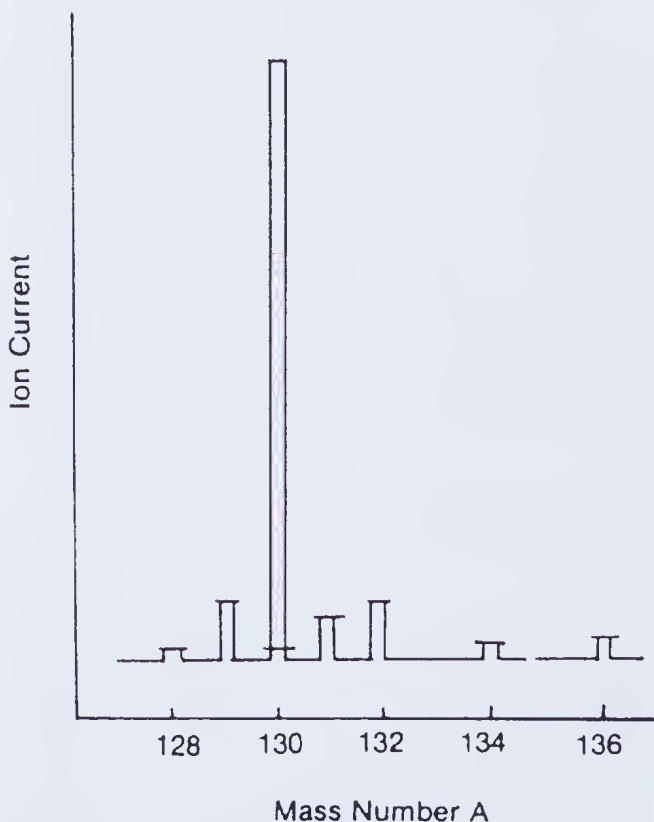
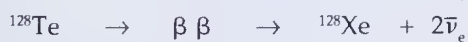
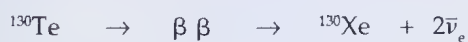


Figure 2. Isotopic composition of xenon extracted from tellurium ore (Kirsten *et al.* 1968). The horizontal lines indicate the maximum contribution of atmospheric xenon.

Geochemical half-life determinations of double beta decay

The geochemical method of measuring double beta decay depends on the accumulation of decay products from this rare nuclear process in a natural mineral of the parent element. The method is most likely to succeed if little of the daughter element was incorporated when the mineral of the parent element formed. The likelihood of this separation occurring in nature is enhanced if the geochemical nature of the double beta decay product is radically different from that of the parent element. Success also depends on the mineral being geologically old and having survived intact over a long period of time so that detectable quantities of the daughter have accumulated in the mineral. Hard, high temperature minerals have a favoured chance of surviving temperature/pressure variations to which the minerals may have been exposed during their geological history.

Geochemical measurements of double beta decay have, until recently, been confined to the measurement of gaseous daughter products (by gas source mass spectrometry), which have accumulated in old tellurium and selenium minerals from the following reactions;



The double beta decay of ^{130}Te to ^{130}Xe is a favourable experimental situation because ^{130}Te is the most abundant nuclide of Te, old telluride minerals of high concentration are available, and the mass spectrometry of Xe can be carried out with high sensitivity. Inghram & Reynolds (1949) first estimated the half-life of ^{130}Te for double beta decay to be 1.4×10^{21} y. Since that time, many ^{130}Te decay experiments have been carried out and a partial list of the results are given in Table 2. The current best estimate of the half-life of ^{130}Te is 8×10^{20} y (Manuel 1991). Figure 2 (taken from Kirsten *et al.* 1968) shows the dominance of ^{130}Xe in the mass spectrum of Xe extracted from an old telluride ore sample. Similar mass spectrometric determinations have been made for the double beta decay half-life of ^{128}Te and ^{82}Se . Manuel

The major analytical shortcoming of the Te/Xe and Se/Kr decay systems is that their daughters are gaseous and therefore may have suffered some leakage from the ore sample over the long time period since the minerals were formed. Minerals of tellurium and selenium are particularly susceptible to gas loss because they are soft, low temperature minerals that may have recrystallised and lost radiogenic Xe or Kr during any deformation event or high temperature phase subsequent to mineralisation. Richardson *et al.* (1986) have shown that gas retention ages are significantly less than mineralisation ages. Lin *et al.* (1986) discuss the problems involved with gas retention in the mineral kitkaite.

Although there may well be uncertainties in the absolute values of ^{128}Te , ^{130}Te and ^{82}Se , there are compelling reasons why the ratio of the half-lives of ^{128}Te , ^{130}Te for double beta decay should be determined. The great advantage of the Te/Xe double beta decay system is that both the daughter products are noble gases and the ratio $^{128}\text{Xe}/^{130}\text{Xe}$, which is directly proportional to the ratio of the half lives of $^{128}\text{Te}/^{130}\text{Te}$, can be determined with relatively high precision by noble gas mass spectrometry, thus eliminating many sources of systematic error.

Pontecorvo (1968) has shown that the ratio of the decay rates of pairs of similar nuclei can be used to test various theoretical predictions because the ratio of their respective matrix elements should be near unity. In the case of Dirac decay, the ratio $\rho_{2v} = \lambda_{2v}^{128}/\lambda_{2v}^{130}$ is much smaller than the Majorana decay ratio $\rho_{0v} = \lambda_{0v}^{128}/\lambda_{0v}^{130}$, where λ is the probability of double beta decay. Thus even a small Majorana decay contribution would cause a drastic increase in the measured ratio $\rho_{\Sigma} = \lambda_{\Sigma}^{128}/\lambda_{\Sigma}^{130}$ above the base level of Dirac decay ρ_{2v} (where Σ represents the sum of the double beta decay mode components).

The measurement of the half-life of the double beta-decay of ^{128}Te is far more difficult than for ^{130}Te because the probability of double beta decay is so much smaller. However, a recent measurement of the double beta decay half lives of ^{128}Te and ^{130}Te (Bernatowicz *et al.* 1993), has determined the daughter product ratio $^{128}\text{Xe}/^{130}\text{Xe}$ with greater confidence than previous measurements listed in Table 3 (Manuel 1991). The mean value for the ratio of half-lives in Table 3 is $4 \cdot 10^{-4}$, which compares favourably with the Bernatowicz *et al.* (1993) value of $3.52 (\pm 0.11) \cdot 10^{-4}$. The data of Bernatowicz *et al.* (1993) give a limit to the effective Majorana mass of the neutrino of 1.5eV.

Table 3

Values reported for the ratio of the double-beta decay rate of ^{128}Te relative to that of ^{130}Te (Manuel 1991)

Reference	$^{130}\text{T}_{1/2} / ^{128}\text{T}_{1/2}$
Hennecke <i>et al.</i> (1975)	$6.3 \cdot 10^{-4}$
Kirsten (1983)	$1.0 \cdot 10^{-4}$
Kirsten <i>et al.</i> (1986)	$1.0 \cdot 10^{-4}$
Manuel (1986)	$5.0 \cdot 10^{-4}$
Takaoka & Sagawa (1988)	$< 6 \cdot 10^{-4}$
Lin <i>et al.</i> (1988)	$3.9 \cdot 10^{-4}$
Takaoka & Sagawa (1990)	$3.2 \cdot 10^{-4}$
Lee <i>et al.</i> (1990)	$4.3 \cdot 10^{-4}$
Current best estimate	$4 \cdot 10^{-4}$

It took 20 years from the time that Pauli first suggested the existence of a neutrino to when Inghram & Reynolds (1949) undertook a determination of the half-life of double beta decay. However, a further 44 years were to elapse before the half-life of double beta decay was measured by solid source mass spectrometry. Improvements in thermal ionisation mass spectrometry have occurred to such an extent over the past decade that it is now possible to conceive of the measurement of the half-life of double beta decay schemes which have a non-gaseous daughter product.

In fact, Kawashima *et al.* (1993) have recently measured the half-life of the double beta decay of ^{96}Mo from

the excess amount of ^{96}Mo found in old zircon samples. A solid source mass spectrometer was adapted to improve the sensitivity for Mo isotopic analyses by the use of ion enhancing media. The resulting half-life for the double beta decay of ^{96}Zr of $3.9 (\pm 0.9) \cdot 10^{19}$ y is lower than the measured half-lives of ^{130}Te and ^{82}Se . Zircons have a particularly tight lattice structure and this property has been successfully exploited in U/Pb geochronology because the radiogenic Pb has remained *in-situ* over extensive geological periods. Unfortunately the presence of U in the zircon samples generate spontaneous fission product Mo which make the measurement of double beta decay ^{96}Mo difficult to identify. Kawashima *et al.* (1993) were forced to assume that the spontaneous fission yields for ^{238}U (which so far have not been measured) are identical to those of the thermal neutron fission of ^{239}Pu to make the necessary corrections. The authors also report a "strange excess" in ^{98}Mo which they were unable to explain. However, despite these difficulties the work of Kawashima *et al.* (1993) has shown that isotopic systems, other than those with gaseous daughters, can be used to measure the half-life for double beta decay.

An examination has been made of the various double beta decay schemes listed by Doi *et al.* (1985) which have non-gaseous daughters. The best candidate seems to be the decay of $^{122,124}\text{Sn} \rightarrow ^{122,124}\text{Te}$. This decay scheme has the advantage that two isotopes can experience double beta decay, old cassiterite samples of known age are available, and the mass spectrometry of tellurium is well established (Loss *et al.* 1990). Furthermore, this system has the great advantage with respect to the Zr/Mo double beta decay system in that cassiterite does not contain a significant amount of uranium, and in any event tellurium is close to the mass valley of nuclear fission where the cumulative fission yields are very low. In addition, cassiterite samples can be converted to the metallic form (McNaughton & Rosman 1991), and ion exchange chemical techniques have been established to separate tellurium from other elements (Loss *et al.* 1990). Doi *et al.* (1985) predict a half-life for ^{124}Sn which is approximately a factor of ten longer than that predicted for ^{96}Zr double beta decay.

It is possible that accelerator mass spectrometry could be applied to the problem of measuring the half-life of double beta decay systems because of this technique's ability to remove molecular interferences and the separation of isobars by rate of energy loss or range measurements. This enables high sensitivity mass spectrometric measurements to be made as an alternative to conventional solid source mass spectrometry, although the necessity for precise determinations of the isotopic composition of the element concerned may present a problem.

Conclusions

It seems surprising that 65 years after Pauli's postulate of the existence of the neutrino, we still do not know some of its basic properties. Neutrinos were produced in huge numbers during the very early stages of the Big Bang, but because of their extremely low interaction with other particles they seem destined to inhabit the Universe as lonely "ghosts of creation". They are also produced copiously from every Main Sequence star, and play an essential role in supernovae explosions (Clayton

1989). Some mass spectrometric evidence to support this latter phenomenon has recently been published (Maas *et al.* 1996). It is a strange quirk of Nature that double beta decay, which is an extremely rare nuclear phenomenon, may be the mechanism which will enable the properties of the neutrino to be better understood. The basic instability of certain r-process nuclides contrasts with their present abundance distribution, which can only be explained if double beta decay rates have an extremely small probability.

The neutrino is the only fermion for which we do not know if it is different from its antiparticle and is therefore a Dirac particle, or if it is identical with its antiparticle and therefore a Majorana particle. Double beta decay offers a novel means of testing Grand Unified Theories of particle physics. In double beta decay two modes are possible – one in which two antineutrinos accompany the emission of two beta particles (the Dirac neutrino) and the second in which no neutrinos are emitted. The clear signature of neutrinoless double beta decay is the emission of two electrons whose combined kinetic energy equals the mass difference between the parent and daughter nuclides. If the latter mode can be experimentally established, it may yield limits on the electron neutrino mass, indicate the degree of lepton conservation in elementary particle interactions and provide fresh evidence for neutrino oscillations. The large difference in half-life between the two modes of double beta decay offers a sensitive indicator of estimating the contribution of neutrinoless decay to the well established two neutrino decay mode.

A considerable body of experimental evidence for the half-life of double beta decay has now been established by both direct counting techniques and geochemical measurements, although the latter technique probably provides an upper limit because of the high probability of gas loss from old tellurium and selenium-rich minerals. However, new geochemical methods based on the detection of solid daughter products by sensitive solid source mass spectrometric techniques should resolve the gas loss problem. Existing evidence suggests that neutrinoless double beta decay does not occur to any significant extent, that the electron neutrino mass may be as small as 1.5eV and that lepton conservation is maintained. However the evidence is fragmentary and plagued by experimental difficulties so that further work, especially on double beta decay, is required.

Acknowledgements: The author acknowledges the technical skills of Ms M Scherer in preparing this paper for publication. Dr J Boldeman and Dr M Zadnik reviewed an earlier draft of this paper and their comments were greatly appreciated. This research has been supported by the Australian Research Council.

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Recent Advances in Science in Western Australia

Earth Sciences

U-series ages using thermal mass ionisation spectrometry (TIMS) are reported by researchers from the Australian National University for Last Interglacial fossil reefs along the stable coastal margin of Western Australia. Reliable ages range from 127 to 122 ka. These and other TIMS observations, combined with glacio-hydro isostatic sea-level models, indicate that the Last Interglacial period occurred from at least 130 to 117 ka. Globally, the main episode of reef growth appears to be confined to a narrow interval from 127 to 122 ka. This may indicate that the Last Interglacial was of short (127 - 122 ka) duration or reflected a major reef-building event in the middle of a longer (130-117 ka) interglacial event.

Stirling CH, Esat TM, McCulloch MT & Lambeck K 1996 High precision U-series dating of corals from Western Australia and implications for the timing and duration of the Last Interglacial. *Earth & Planetary Science Letters* 135:115-130.

Researchers from Western Mining (Melbourne), the University of Adelaide, and Queens University (Ontario) describe how numerous palaeovalleys formed extensive drowned estuaries during Eocene transgressions along the south-western part of the southern margin of Australia. The Norseman Formation in the Cowan palaeovalley was deposited during the Middle Eocene Tortachilla transgression. Initial deposition was of sands and gravels, followed by pure carbonates during the highstand, produced by a typical shallow temperate water assemblage of bryozoans, coralline algae, echinoids and molluscs swept into shoals by strong tidal currents. Spencer Gulf and Gulf St Vincent of South Australia provide close modern analogues of the Cowan palaeovalley, and the Norseman Formation is an excellent example of cool-water carbonate deposition in near-shore tide-dominated environments.

Clarke JDA, Bone Y & James NP 1996 Cool-water carbonates in an Eocene palaeoestuary, Norseman Formation, Western Australia. *Sedimentary Geology* 101:213-226.

An 'evaporative concentration-lateral groundwater flow' model is proposed by researchers from AGSO and CSIRO Division of Water Resources (Canberra) for the formation of Cu-(Pb-Zn) sulfides during a depositional cycle of carbonates in restricted marine environments using data from the Nilemah Embayment, Shark Bay. The model is constrained by; (i) the short time available for ore accumulation during a single depositional cycle, (ii) limitation of adequate rates of bacterial sulfate reduction for the formation of an ore deposit to near-surface sediments; (iii) restriction of the most favourable ore-forming sites to the intertidal zone and the littoral shelf; (iv) coincidence in these sites of *in situ* cyanobacterial mats and shallow erosional depressions containing detrital organic matter eroded from the mats. Under these conditions, the metalliferous fluid would have to contain about 1000 ppm Cu and flow for 1000 years at a rate of 5 m/a through the intertidal/littoral environment to produce an ore deposit.

Ferguson J & Skyring GW 1995 Redbed-associated sabkhas and tidal flats at Shark Bay, Western Australia: their significance for genetic models of stratiform Cu-(Pb-Zn) deposits. *Australian Journal of Earth Sciences* 42:321-333.

Four major plutonic episodes have been identified by researchers from the Geological Survey of Western Australia and Australian National University, at ca 2630 Ma, 1700-1600 Ma, 1300 and 1160 Ma. Orthogneiss, largely derived from the ca 2630 Ma and 1700-1600 Ma granitic precursors, forms a belt along the south-eastern margin of the Yilgarn Craton. These rocks, together with the gabbro of the Fraser Complex, were intruded by granitic magmas and metamorphosed in the granulite facies at ca 1300 Ma. They were then rapidly uplifted and transported westward along low-angle thrust faults over the south-eastern margin of the Yilgarn Craton. Between ca 1190 and 1130 Ma, granitic magmas were intruded throughout the eastern part of the orogen. Comparison with rocks on the Antarctic coast between Casey and the Bunger Hills shows that the southern part of the Albany-Fraser Orogen may be found here, and that the 1700-1600 Ma orthogneisses identified in the eastern Albany-Fraser Orogen may have originally formed part of an east Antarctic continent that was thrust onto the margin of the Yilgarn Craton during the collision of these two continents at 1800 Ma.

Nelson DR, Myers JS & Nutman AP 1995 Chronology and evolution of the Middle Proterozoic Albany-Fraser Orogen, Western Australia. *Australian Journal of Earth Sciences* 42:481-495.

The distribution of mafic/ultramafic sills described by W K Witt of the Geological Survey of Western Australia is consistent with models that envisage the Kalgoorlie Terrane (abundant komatiitic and MORB-like tholeiitic volcanics and intrusive equivalents) as an ancient continental marine basin. Plagioclase-rich (leucodolerite) sills in the Melita area (Gindalbie Terrane) have alumina-rich TiO₂-poor compositions comparable to island-arc tholeiites and were derived by partial melting of an enriched mantle source. The geochemistry and distribution of sills is not compatible with a simple, craton-scale plume model for the formation of the greenstone belts.

Witt WK 1995 Tholeiitic and high-Mg mafic/ultramafic sills in the Eastern Goldfields Province, Western Australia: Implications for tectonic settings. *Australian Journal of Earth Sciences* 42:407-422.

Deformation documented by a team of scientists from the Geological Survey of Western Australia, BHP Minerals and the University of Western Australia, for the Upper Devonian carbonate rocks of the Lennard Shelf shows a complex history involving synsedimentary structures and faults. In the Pilbara Range-Limestone Billy Hills region, a corridor of north-east-trending deformation is associated with dextral offset of the reef margins, and is interpreted as an accommodation zone comprising an echelon of sinistral oblique-slip faults, probably above basement faults at depth. The distribution of lithofacies is controlled by basement-hosted faults, with the reef and platform facies confined to palaeo-highs. The gross structural architecture of the Lennard Shelf appears to be of strike-extensive north-west-trending listric normal faults that parallel the basin margin and which show apparent offset on north-east-trending zones of accommodation structures. There is no

evidence for compressional tectonics nor penetrative deformation as suggested by some earlier workers.

Döring SL, Dentith MC, Groves DI, Playford PE, Veamcombe JR, Muhling P & Windrim D 1996 Heterogeneous brittle deformation in the Devonian carbonate rocks of the Pilbara Range, Canning Basin: Implications for the structural evolution of the Lennard Shelf. *Australian Journal of Earth Sciences* 43:415-429.

Life Sciences

The relative growth rate, mortality and stem form of individual trees in mixed stands of planted *Pinus radiata* and regenerated *Eucalyptus obliqua* were investigated by foresters, from the State Forests of NSW and the University of Melbourne. Relative growth rate increased with tree size and decreased with higher neighbourhood leaf area, and increased with higher neighbourhood density as a result of release from competition. The growth, mortality and changes in stem form led to changes in density-dependent stand characteristics such as mean height-to-diameter ratio and size-distribution patterns.

Bi H & Turvey ND 1996 Competition in mixed stands of *Pinus radiata* and *Eucalyptus obliqua*. *Journal of Applied Ecology* 33:87-99.

Field-screening of cucumber mosaic virus (CMV), which is seed-transmitted in narrow-leaf lupin *Lupinus angustifolius*, was developed by researchers from the Plant Industries Division (WA Department of Agriculture), based on spreader rows, where a susceptible Wandoo cultivar was grown on either side of each test row. Ten lines of lupin were categorised into moderately-resistant, moderately-susceptible, susceptible and very susceptible categories; no lines were highly resistant. Breeding for low CMV seed transmission rates is recommended, and advanced breeding lines with unacceptably high intrinsic transmission rates (>20%) should be culled out.

Jones RAC & Cowling WA 1995 Resistance to seed transmission of cucumber mosaic virus in narrow-leaved lupins (*Lupinus angustifolius*). *Australian Journal of Agricultural Research* 46:1339-1352.

Examination of the canopy arthropod communities of eucalypt trees in eastern and western Australia, determined at 3 month intervals using chemical knock-down procedures, revealed that arthropods were more common in eastern Australian trees and that there was a different seasonal pattern. The phenological patterns of canopy arthropods appear to be related to the condition of the host trees and/or climatic factors. Detection of variability in seasonal and annual patterns of canopy invertebrate communities by long-term sampling is required to evaluate the impact of disturbances on forest communities.

Recher HF, Majer JD & Ganesh S 1996 Seasonality of canopy invertebrate communities in eucalypt forests of eastern and western Australia. *Australian Journal of Ecology* 21:64-80.

Volume 4 of Monographs on Australian Lepidoptera, The Checklist of the Lepidoptera of Australia, provides the first complete documentation of this taxon, including nomenclature and classification for all of the entire named Australian lepidopterans. Generated from a computer database compiled with strict protocols, it includes over 24660 names. There is an introduction to each fam-

ily. It records over 850 significant misspellings, over 1250 new synonymies and over 1500 new combinations. A CD-ROM of all text files is included.

Nielsen ES, Edwards ED & Rangsi TV (eds) 1996 Checklist of the Lepidoptera of Australia. Vol 4, Monographs on Australian Lepidoptera. CSIRO Publishing, East Melbourne.

Resource partitioning within an assemblage of seven species of insectivorous birds, inhabiting remnant *Melaleuca* woodland on Rottnest island, was examined by researchers from Murdoch University. Foraging habits of birds were found to be both species-specific and associated with the month of observation, indicating that foraging partitioning occurred but the pattern varied temporally. The diversity of foraging habitats of each species varied widely in each foraging dimension, although species which were generalists in one foraging dimension tended to also be generalists in other dimensions.

Wheeler AG & Calver MC 1996 Resource partitioning in an island community of insectivorous birds during winter. *Emu* 96:23-31.

Assessment of the growth and yield of 97 seedlots of Gungurru narrow-leaf lupins, for seed size, percentage germination, cucumber mosaic virus (CMV) seed infection, and several seed nutrients, showed that plant density, shoot dry weight at 6 weeks, and grain yield varied significantly among seedlots. Seed size influenced stand density and shoot dry weight, but not grain yield. No seed nutrient was strongly associated with grain yield. There was no association of seedlot with the geographical source of the seed. High germination percentage and low CMV infection were the main predictors of high grain yield, but accounted for only 40% of the variance among seedlots in yield.

Tapscott HL & Cowling WA 1995 Predictors of yield of *Lupinus angustifolius* (cv. Gungurru) seedlots from different sources in Western Australia. *Australian Journal of Experimental Agriculture* 35:745-751.

Evidence of the natural fire frequency to which *Banksia hookeriana* was best adapted, was sought through analysis of its seed demography. Plants begin flowering at 3-4 years, but storage of viable seeds in the canopy was rare for plants less than 5 years old. Cones contained an average of 12 follicles, holding 2 seeds; 62% of seeds were estimated to be viable. Cone production increased with age, to about 17 cones per year at an age of 15 years. Seed was lost by spontaneous follicle rupture, granivory, and decay. A seed bank computer model predicted continued seed accumulation to at least 25 years of age, but by this time more seeds had been lost than were stored. Over many generations, the likelihood of successful recruitment occurs for an average fire frequency of 15-18 years. Recent fires have recurred within 7-11 years, indicating a human impact on the natural fire regime which may ultimately threaten *Banksia hookeriana*.

Enright NJ, Lamont BB & Marsula R 1996 Canopy seed bank dynamics and optimum fire regime for the highly serotinous shrub, *Banksia hookeriana*. *Journal of Ecology* 84:9-17.

Cooperative research between the University of Western Australia and the Western Australian Museum used allozyme and morphometric variability to provide a genetic perspective of the Indonesian fruit bat genus *Cynopterus*. The genetic distance between populations of

C. nusatenggara was strongly correlated with both the contemporary sea-crossing distance between islands, and the estimated sea-crossing distance at the last Pleistocene glacial maximum. This, and the low levels of population substructure within islands, indicates that the sea is a primary and formidable barrier to gene exchange. Morphometric variability did not show any of the main effects seen in the genetic data, suggesting that genetic and morphometric variability were not associated at the level of individuals.

Schmitt LH, Kitchener DJ & How RA 1995 A genetic perspective of mammalian variation and evolution in the Indonesian Archipelago: Biogeographic correlates in the fruit bat genus *Cynopterus*. *Evolution* 49:399-412.

The present environment of Australia represents a palimpsest that records a history of past climates, nutrient poor soils, burning and increasing aridity, but these details of history are not easily disentangled. Present observations cannot be readily used to interpret the past environments, and to infer these it is necessary to consider geological, climatic and weathering histories, as well as the physiological development of the structures being used as evidence. It is argued that the origins of fire-adaptation may predate the arrival of Aborigines, whose use of fire in cultural and hunting practices has only influenced the biota for about 50000 years. This is too short a time to have influenced the biota, other than to eliminate or winnow out those elements unable to cope with the new fire regimes.

Main AR 1996 Ghosts of the past: Where does environmental history begin? *Environment & History* 2:97-114.

Change in the number of red kangaroos in the pastoral zone of South Australia is related by a researcher from the University of Melbourne to rainfall and population size. Because of uncertainty about the responses of red kangaroo populations to rainfall, it is difficult to analyse the effects of harvesting on the kangaroos. The effects of rainfall and population size depend on the scale of observation; the previous year's rainfall is closely related to population changes over large areas, but summer and autumn rainfall is more critical over smaller areas.

McCarthy MA 1996 Red kangaroo (*Macropus rufus*) dynamics: Effects of rainfall, density dependence, harvesting and environmental stochasticity. *Journal of Applied Ecology* 33:45-53.

The authoritative volumes on Protura, Collembola and Diplura (Volume 22), and Echinodermata (Volume 33) of Australia are part of the Zoological Catalogue of Australia, a computer database of taxonomic and biological knowledge of the Australian Fauna. This 90-odd volume Catalogue, produced as a public inquiry database, serves as a comprehensive directory to recent information on each species of the Australian fauna. Information on each species includes synonymy, literature citation, location and status of type material and type locality, a brief summary of geographical distribution, ecological attributes, and important references including basic biology.

Houston WWK & Greenslade P 1994 Protura, Collembola and Diplura. Volume 22. Zoological Catalogue of Australia. Australian Biological Resources Study, Canberra.

Rowe FEW & Gates 1996 Echinodermata. Volume 33. Zoological Catalogue of Australia. Australian Biological Resources Study, Canberra.

Papers from the Sixth International Theriological Congress have been published in the March issue of Volume 21 of the *Australian Journal of Ecology*:

Oates JF 1996 Habitat alteration, hunting and the conservation of folivorous primates in African forests. *Australian Journal of Ecology* 21:1-9.

Cork SJ 1996 Optimal digestive strategies for arboreal herbivorous mammals in contrasting forest types: Why koalas and colobines are different. *Australian Journal of Ecology* 21:10-20.

Braithwaite LW 1996 Conservation of arboreal herbivores: The Australian scene. *Australian Journal of Ecology* 21:21-30.

Smith AP & Ganzhorn JU 1996 Convergence in community structure and dietary adaptation in Australian possums and gliders and Malagasy lemurs. *Australian Journal of Ecology* 21:31-46.

Physical Sciences

Note from the Hon Editor: This column helps to link the various disciplines and inform others of the broad spectrum of achievements of WA scientists (or others writing about WA). Contributions to "Recent Advances in Science in Western Australia" are welcome, and may include papers that have caught your attention or that you believe may interest other scientists in Western Australia and abroad. They are usually papers in refereed journals, or books, chapters and reviews. Abstracts from conference proceedings will not be accepted. Please submit either a reprint of the paper, or a short (2-3 sentences) summary of a recent paper together with a copy of the authors' names and addresses, to the Hon Editor or a member of the Publications Committee:

Dr P C Withers (Hon Editor), Department of Zoology, University of Western Australia, Nedlands WA 6907

Dr S D Hopper (Life Sciences), Kings Park and Botanic Garden, West Perth WA 6004

Dr A E Cockbain (Earth Sciences), PO Box 8114, Angelo Street, South Perth WA 6151

Assoc Prof G Hefter (Physical Sciences), Mathematical and Physical Sciences, Murdoch University, Murdoch WA 6150

Final choice of articles is at the discretion of the Honorary Editor.

"Letters to the Editor" concerning scientific issues of relevance to this journal are also published, at the discretion of the Hon Editor. Please submit a word processing disk with letters, and suggest potential reviewers or respondents to your letter.

P C Withers, *Honorary Editor, Journal of the Royal Society of Western Australia*.

c/o Western Australian Museum, Francis Street, Perth WA 6000

Installation of Professor Michael Jones as the new President of the Royal Society of Western Australia.

His Excellency Major General Michael Jeffery, AC MC
Governor of Western Australia.



Vice-Patron of The Royal Society of Western Australia

Monday 15 July, 1996

*Dr Steve Hopper, Outgoing President of the Royal
Society of Western Australia
Professor Michael Jones, Incoming President of the
Royal Society of Western Australia
Distinguished Guests, Ladies and Gentlemen*

It is my pleasure to be here tonight to attend your Annual General Meeting and to install the Incoming President, Professor Michael Jones.

The Royal Society of Western Australia has the very real potential, and indeed I would suggest the responsibility, to play a very important role in Society in influencing the community and governments of the critical importance of science and research, if Australia wishes to remain the 'Lucky Country'.

In recent years, science appeared to be losing its appeal for children, and while many young people were concerned, few seemed to be aware of the role that science played in their daily lives. Many appeared to associate science with pollution and nuclear accidents, like Chernobyl, and saw scientists as underpaid and undervalued.

Thankfully, places like Scitech and the weekend morning children's television show 'Hot Science', which present science as a wonderful, glamorous and exciting subject, and organisations like the Royal Society of Western Australia, a body of distinguished scientists and scholars whose primary objective is to promote learning and research in the natural and social sciences and in the humanities, are doing much to change this image.

The Western Australia Education Department has instigated its own policy to encourage science, while science teachers and engineering associations hold competitions such as the annual 'Tournament of Minds' to encourage and stimulate young students to discover creative solutions to problems.

For example, from February 1995 to last month, a total of 240 State Primary Schools implemented, or were in the process of implementing, the Australian Academy of Science 'Primary Investigations' Program. The success of the program has been due to cooperation and collaboration between the Education Department and the science education community. An external evaluation of the effectiveness of the program indicated that, in general, the program

- raised the status of science in primary schools;
- resulted in a whole school approach to science;
- increased student interest in science; and
- resulted in reluctant teachers teaching science.

Its effectiveness has been recognised nationally as indicated by the following statement from the Australian Academy of Science;

"By 1999, at least 50% of Australian primary schools should have structured, whole-school science programs, with 100% involvement by 2002. One state, Western Australia, is already close to achieving the 1999 target."

A science content course for science teachers has also been established.

At the high school level, a Secondary School Teacher Leaders Program was established last year, to train 14 experienced secondary teachers in science education theory and its applications to classroom best practice. Each of these teachers was supported in testing out the ideas presented, sharing their work with others in the group and staff at their schools, and in initiating programs to suit the needs of their students.

Many of the teachers trained last year are continuing their training this year, and two additional programs have been established. One is for experienced teachers, and the other is for science Heads of Department.

Last year, the number of students awarded grades for year 12 science courses were;

Biology 2476 (14.3% of year 12 students),
Chemistry 4132 (23.87%),
Geology 95 (0.54%),
Human Biology 5070 (29.29%),
Physical Science 532 (3.07%),
Physics (3132 (18.09%), and
Senior Science 2052 (11.85%).

In a world where the population is expected to reach 10 billion over the next few decades and where people will live to an older age, we are going to need more scientists to tackle problems such as nuclear radiation from damaged power plants, such as at Chernobyl, and leaks from sunken nuclear submarines; agricultural shortages in South East Asia, where China for example will have to annually import 370 million tonnes of grain by the year 2030, and Indonesia which was self-sufficient in rice production from 1984 to 1994 has had to start importing rice again, to make up for shortfalls caused by drought, disease and conversion of rice land to other uses; the salinity problems in the Murray/Darling Basin and our own Wheatbelt; vehicle emissions and pollution worldwide; the Greenhouse effect, marine and air pollution, land degradation, conservation of the natural

environment, retention of biodiversity, protection of forests, over-population, water quality and energy options. There will be substantial opportunities for new environment-friendly technologies, such as waste munchers, water purifiers and solar power.

Western Australia offers wonderful opportunities for research in a range of sciences, from those that support industries like mining and petroleum, through to botanists who can explore one of the richest floras in the world, with the potential to yield new natural medicines.

Australia is so different in its geological origins and history that scientists have a superb opportunity to make new discoveries.

On the home front, we will need to maintain our place in competitive international markets and meet the immediate challenge of being 'APEC-ready' by 2010, when the expected free trade agreement will have maximum impact on Australia's international performance. Australia needs to address many difficult issues in managing the rapid pace of scientific and technological change, as it confronts the forces shaping our long-term economic future.

We can no longer rely on natural resources for Australia's wealth and long-term prosperity in a complex world where technologies that did not exist a few decades ago are playing important roles in our social and economic life. For example, twenty years ago many students could expect to leave school and move into a job in the clerical field while continuing their studies. The advent of electronic mail, fax machines, mobile phones, CD-ROM, the Internet, multi-media and computer networks is seeing the rapid demise of the office boy or girl, thus resulting in fewer jobs for today's school leavers.

While the development, acquisition and application of knowledge through science, technology and innovation can create new sources of wealth and improve the quality of our lives, it also raises some serious social issues. For example, it has been suggested that partly due to technology, of our 757,100 Australians out of work as of last month (74,200 in Western Australia), many may never work again. They simply will not be employable, and nor might their children.

Is this going to be an irreconcilable fact of life, with its serious social consequences for the foreseeable future, or can we through genuine intellectual endeavour meet the technology challenges of a modern society with a corresponding social conscience? It will, I think, be important for the scientist of the future to have a well-developed social conscience.

In all its work, The Royal Society of Western Australia aims to bring together an informed and scholarly approach to scientific and technological questions. Its work aims to improve the links between the science and technology community and the education sector from pre-school to tertiary levels.

The Royal Society of Western Australia contributes to the advancement of science for the good of Western Australia by;

- providing a forum for discussion of scientific and technological issues relevant to the community,
- bridging the communication gap between scientific disciplines, and

- bringing significant scientific and technological issues to the attention of government and other decision makers.

I believe that The Royal Society has the potential to utilise its wealth of talent to influence decision makers toward a more dedicated approach towards science education.

The Royal Society of Western Australia has been very fortunate in having Dr Steve Hopper as President for the past year. Dr Hopper is Director and Chief Executive Officer of Kings Park and Botanic Garden. After 14 years as a research scientist working on the conservation of Western Australian flora, Dr Hopper moved into research administration as officer-in-charge of the Western Australian Wildlife Centre, before his appointment at Kings Park and Botanic Gardens in 1992. He has developed specialist expertise in the fields of rare and endangered plants, urban bushland conservation, and the biology of eucalypts, orchids and kangaroo paws. In 1990, he travelled to the United States of America on a Fullbright Senior Scholar's Award, and served as a Miller Visiting Research Professor at the University of California, Berkeley. At Kings Park and Botanic Gardens, Dr Hopper has led strategic planning and new works aimed at delivering world-class services and facilities within 10 years. As Vice-Patron of The Royal Society of Western Australia, I would like to extend my thanks on behalf of The Society to Dr Hopper for his dedication to The Society, especially in the past year as President.

Professor Michael Jones attended Cambridge University, graduating in Natural Sciences (Biochemistry) followed by a Ph. D. in plant biochemistry. This was followed by postdoctoral research fellowships at the University of Missouri (Plant Pathology), the Australian National University (Developmental Biology) and then back to Cambridge University (Biochemistry). He was then appointed senior scientific officer at the Welsh Plant Breeding Station (1979-1982) and principle Scientific Officer at Rothamsted Experimental Station, United Kingdom (1982-1990). In November 1990, Professor Jones was appointed to Murdoch University and became Head of the Plant Sciences discipline within the School of Biological and Environmental Sciences. In 1994, he was appointed Director of the Western Australia State Agricultural Biotechnology Centre, and from this month Professor Jones has been released from his duties within Plant Science to act as full-time director of the Western Australian State Agricultural Biotechnology Centre. I extend my best wishes to Professor Jones for his term as President. As Vice-Patron of The Royal Society of Western Australia, I very much look forward to furthering my association with The Society and its new president in the coming year.

It is now my very agreeable duty to call upon you, Professor Michael Jones, to be installed as the President of The Royal Society of Western Australia. As the President, you are a member of the Council and you preside over all meetings of The Council and Society. I charge you to carry out diligently and faithfully your responsibilities, and to foster the study of science for the good of the global community. Professor Michael Jones, it gives me great pleasure to formally install you as the President of The Royal Society of Western Australia.

The impact of vegetated buffer zones on water and nutrient flow into Lake Clifton, Western Australia

P M Davies¹ & J A K Lane²

¹Department of Zoology, The University of Western Australia
Nedlands, WA 6907

²Department of Conservation and Land Management
Wildlife Research Centre, PO Box 51 Wanneroo, WA 6065

Manuscript received October 1995; accepted March 1996

Abstract

Lake Clifton, a saline lake situated on the Swan Coastal Plain, south of Perth, is recognised under the Ramsar Convention as a "Wetland of International Importance". Intensification of rural and urban developments along the eastern catchment of the lake have been implicated in increased nutrient levels and consequent algal growth in the water. This has adversely affected a highly-restricted microbialite population which is the largest in the southern hemisphere. Existing buffer zones of native vegetation separate the cultural developments from the lake, and have the potential to reduce impacts both by the uptake of surface-water flow and the assimilation of nutrients. These buffer zones can be divided into three categories based on width; small (20-50 m), medium (100-150 m), and large (500-600 m).

Surface-water flow into Lake Clifton from the buffer zones was highly episodic, occurring predominantly during and immediately after rainfall events of >10 mm rainfall over a 48 hour period. During six substantial rainfall events (May to September 1993), surface flow into the lake (located using a low-flying aircraft) was measured for rates of instantaneous water discharge and water samples were taken for nutrient analyses. Surface water discharge from small buffer zones was about 100 times higher and total nitrogen content was significantly greater compared with the other buffer zones. Although not statistically different, mean levels of total phosphorus ranged from 0.16, 0.04 and 0.07 mg L⁻¹ from the small, medium and large zones respectively.

Our results suggest that the existing buffer zones, particularly those classified as small, are inadequate to limit nutrient input into Lake Clifton. The inadequacy of these buffer zones is mitigated, in part, by the small volumes of water flowing into the lake via surface discharge. However, unless wide buffer zones are provided, further development in the catchment will increase the rate of eutrophication of Lake Clifton.

Introduction

Lake Clifton is part of the Peel-Yalgorup system on the western edge of the Swan Coastal Plain, approximately 100 km south of Perth. The environmental significance of this Ramsar-listed lake is based, in part, on an extensive (400 ha) living microbialite (thrombolite) community that is the largest known in the southern hemisphere (Moore *et al.* 1983; CALM 1990). The presence of microbialites along the eastern shore of the Lake has been attributed to constant discharge of low salinity, highly alkaline groundwater (Moore *et al.* 1983; Moore 1987; Moore & Turner 1988).

Lake Clifton lies within Yalgorup National Park, but only the lake basin and a very narrow margin of land are protected. Much of the land on the eastern catchment is privately owned and used for livestock and horticultural purposes (Moore & Turner 1988), and more recently for urban developments. There has been considerable concern expressed that survival of the microbialite community may be threatened by increasing nutrient inputs from these cultural developments, and that buffer zones may not be substantial enough to reduce nutrient

movement into the lake. Excessive nutrient inputs have already been implicated in increased growth of a green alga (*Cladophora vagabunda*) which, along with epiphytic algae and plankton blooms, smothers and spatially competes with microbialites (Moore 1990).

There are a number of mechanisms whereby nutrients enter the lake, the two major ones being overland flow and groundwater discharge. Overland flow is episodic, occurring after substantial rainfall events, while groundwater input is relatively more constant. Preliminary results have shown that the groundwater typically has a lower total nitrogen concentration than Lake Clifton water (Moore & Turner 1988). However, surface water has not yet been monitored for rates of discharge and associated nutrient levels. Surface flow may be intercepted by vegetated buffer zones, reducing the impact of land practices on a wetland.

Buffer zones are generally described as areas of undeveloped, vegetated land extending from the banks or high water level of a wetland to some landward point (Palfrey & Bradley 1990); the function of a buffer zone is to protect a wetland from negative impacts of catchment land-uses (Carter 1992). Buffer zones around wetlands are valuable as biological filters of both sediment and nutrients. These zones can reduce the extent of channelised surface-flow into a lake and have an inher-

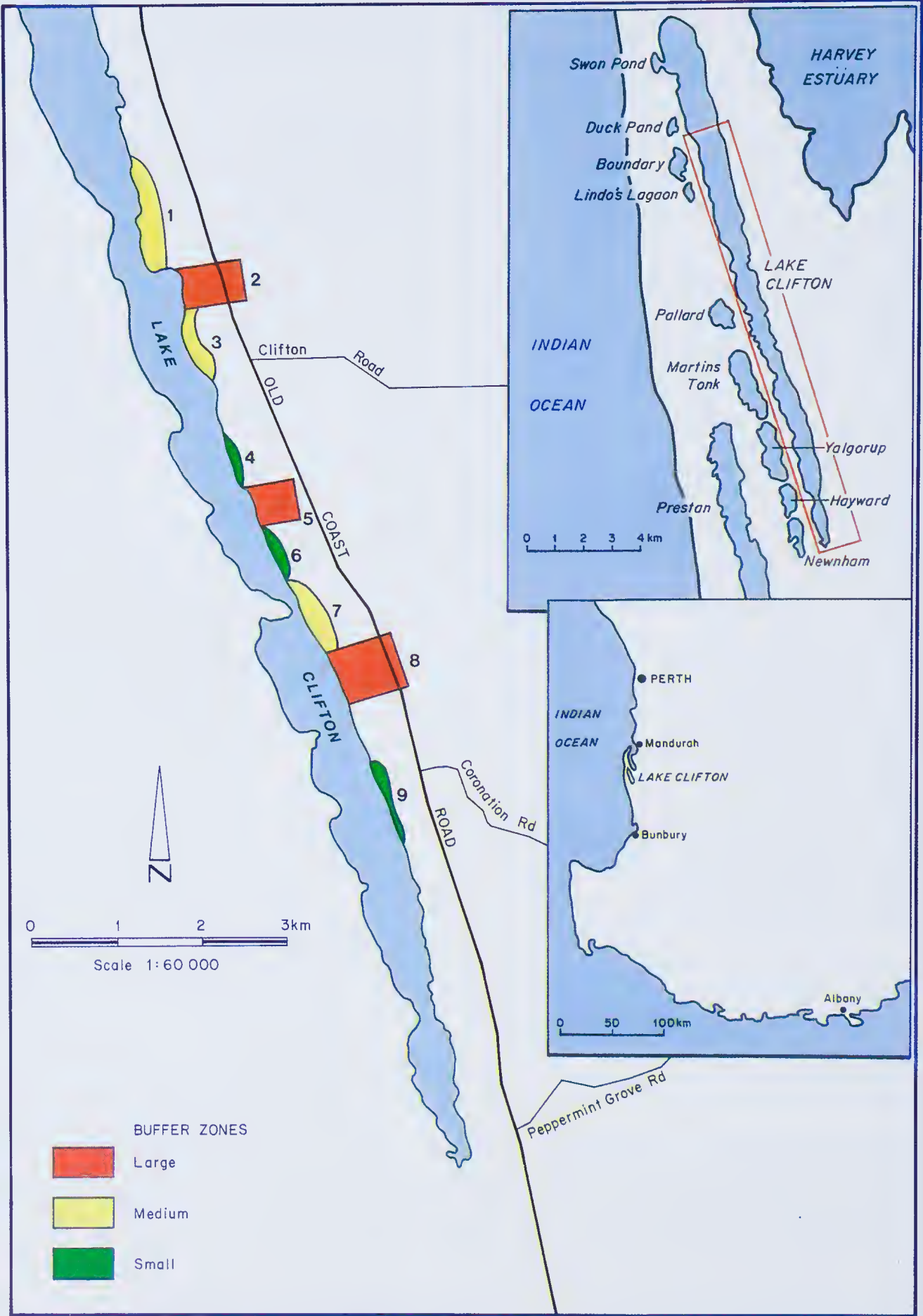


Figure 1. The study sites along the eastern edge of Lake Clifton. Sites as follows: 2,5,8 (large [L]), 1,3,7 (medium [M]) and 4,6,9 (small [S]).

ent capacity to assimilate nutrients and sediment (Davies & Lane 1995). Buffer zones of native vegetation, of varying widths, have been created along the eastern edge of Lake Clifton around rural land-use areas and, recently, urban sub-divisions. This presented an opportunity to compare the effectiveness of buffer zones of different widths in reducing both water discharge and nutrient inputs into Lake Clifton.

Methods

Site description

Lake Clifton is an elongate (approximately 28 km x 1 km), shallow and saline lake about 100 km south of Perth on the Swan Coastal Plain (Fig 1). The extensive shoreline means there is considerable potential for nutrient enrichment from adjacent land practises.

Sampling program

There are no major drains flowing into Lake Clifton (Moore *et al.* 1983). However, previous observations revealed that surface water becomes channelised and flows into the lake after substantial rainfall events. Substantial rainfall events were defined by analysing historical rainfall records for Mandurah (Bureau of Meteorology, Perth). On the basis of this analysis, events of >10 mm rainfall over a 48 hour period were determined to be "substantial". Sampling was then conducted on six of these events (Table 1), which accounted for almost 20% of the 1993 total rainfall.

During each sampling occasion, the eastern edge of the lake was observed from a low-flying aircraft to determine areas where surface water was channelised and flowed into the lake. Channelised surface flow was defined as stream-flow originating within each buffer zone and flowing into the lake. Channelised flow did not originate from outside the boundary of any buffer zone. Existing buffer zones along the eastern edge of the lake, from the airstrip in the north (site 1) to Location 52 in the south (site 9) (approximately 10 km), were placed into three width categories (Fig 1); small, 20-50 m; medium, 100-150 m; and large, 500-600 m wide.

A total of nine buffer zones were investigated, with three from each of the above categories. The zones were approximately the same length (see Fig 1). These buffer zones were interspersed, minimising the effects of spatial

arrangement confounding the subsequent statistical comparisons. Additionally, there were no land-use areas associated with only a single buffer category, which could also have confounded the results. Flow from these zones accounted for the total visible surface flow into the lake. The extreme south-east corner was inaccessible to sampling; however, surface water flow from this area into the lake appeared to be minimal.

Instantaneous channelised discharge from each site was estimated from the rate of water flow and its width and depth. The rate of flow was measured by a Marsh-McBirney 201M model field water-flow meter. Where the water was not of sufficient depth for the meter to operate, discharge was estimated by the time taken to fill a plastic 1 litre measuring cylinder.

Water samples were collected from each site for the analyses of total nitrogen, ammonia, nitrite and nitrate, and total phosphorus and orthophosphate. Unfiltered water samples were collected into sterile 250 ml plastic bottles for measurement of total nitrogen and total phosphorus. Water samples filtered through a 0.22 µm millipore filter into a 100 ml sterile plastic bottle were collected for the measurement of ammonium, nitrate and orthophosphate. Due to costs of each analyses, ammonium, nitrate and orthophosphate were not measured from all sites, with analysis restricted to one sample from each buffer-width category on each occasion. Within each buffer zone where channelised flow was evident from more than one area, nutrient sampling was conducted from a randomly-determined location. However, total discharge was estimated by measuring flow from all channelised flow within each buffer zone. Samples of lake water for nutrient analyses were taken adjacent to one of the large buffer zones (site 8). All samples were kept on ice prior to delivery to the Chemistry Centre of Western Australia for analyses.

Data analyses

All data were plotted prior to parametric analyses to check for normality, and bivariate plots were examined to determine possible non-linear relationships between variables. Statistical comparisons between means were made by Analysis of Variance (ANOVA); Cochran's C was used to test for homogeneity of variances and appropriate transformations were made for biased data, *e.g.* log(*x*), or log(*x*+1) if data contained zero values. After ANOVA, if there was a significant difference, a Tukey's test was used to find which factors or sites were different. Tukey's tests have been recommended for *post hoc* significance testing as a method using the correct experiment-wise error rate (Day & Quinn 1989).

Results

Lake Clifton is within a region of Western Australia typified by a mediterranean climate (Seddon 1972) where rainfall occurs predominantly from late autumn to early spring. Rainfall in 1993 for Yalgorup National Park (Fig 2) followed this pattern although storms during early autumn and late spring delivered substantial rainfall. The total rainfall in 1993 was 688 mm, which is substantially less than the average 1982-1992 annual rainfall of 780 mm.

Table 1

Sampling dates and associated 48 hour rainfall data for Yalgorup National Park during 1993.

SAMPLING DATES	ACRONYM	RAINFALL (mm over 48 h)
28 May 1993	MAY	28
29 June 1993	JUN	19
28 July 1993	JUL	34
25 August 1993	AUG	12
7 September 1993	SEP	17
30 September 1993	OCT	12

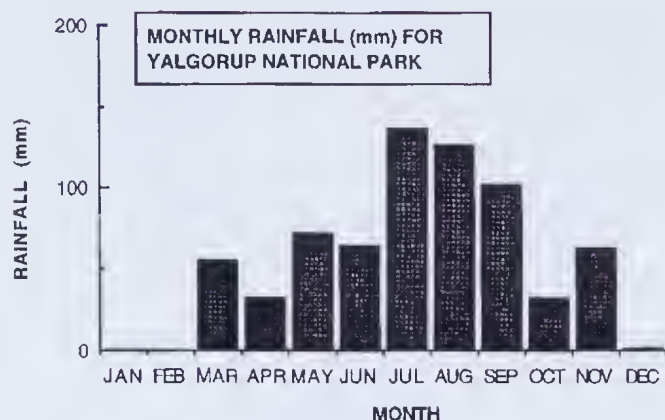


Figure 2. Monthly rainfall for Yalgorup National Park (which incorporates Lake Clifton) during 1993.

Surface runoff

Rates of discharge from the small buffer zones were about four times those of the medium-sized buffer zones and about 100 times those of the large buffer zones (Fig 3). Runoff from the large buffer zones was negligible, with the exception of site 8 (see Fig 1) which was subsequently the only large buffer zone sampled. This area had been burnt prior to the May sampling period, removing the majority of the understorey. This may have contributed to the extent of the measured surface runoff.

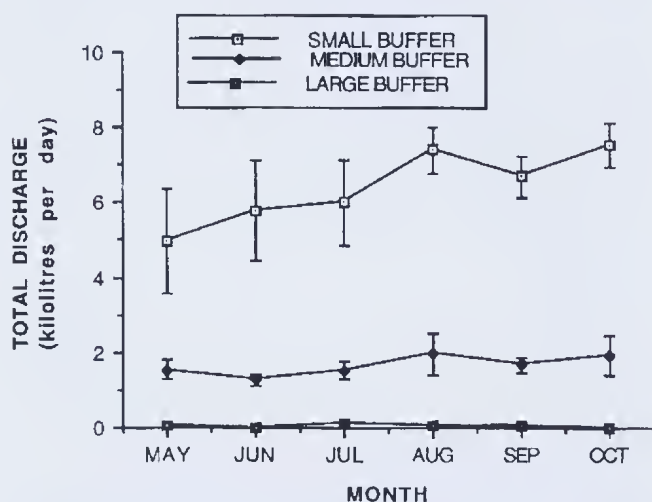


Figure 3. Mean ($\pm$ SEM) surface runoff (in kilolitres per day) from the three different-sized buffer zones during each sampling occasion. Sampling sizes for the small and medium buffers, $n = 3$ on each occasion. A single sample was taken from the large buffer zones (site 8).

The measured surface water runoff contributed little to the total lake water levels. Determining the area of Lake Clifton from aerial photographs, and assuming an annual mean depth of 1 m, enabled the estimation of the mean water volume of the lake. Assuming that the mean surface flow measured during the substantial rainfall events was constant for six months of the year, this flow would contribute only about 0.005% to the total lake volume. This emphasises the importance of sources of water inputs other than surface flow for the maintenance of lake water levels.

Nitrogen concentration in surface runoff

In surface runoff, total nitrogen concentration ranged

Table 2

Mean (SEM) levels of total nitrogen (mg L^{-1}) from the three different buffer sizes and from Lake Clifton during the six sampling periods. Sampling size for the small and medium buffers, $n = 3$ on each occasion. One sample was collected from the lake and from a large buffer zone (site 8) on each occasion.

MONTH	SMALL	MEDIUM	LARGE	LAKE
MAY	31.56 (26.67)	4.17 (1.24)	11.00	1.7
JUN	4.50 (0.40)	4.43 (1.58)	20.00	1.1
JUL	5.90 (1.10)	5.53 (1.01)	0.48	1.3
AUG	13.50 (7.99)	3.80 (1.45)	0.27	1.1
SEP	13.43 (9.76)	0.90 (0.15)	1.50	1.0
OCT	3.17 (0.91)	1.28 (0.44)	4.80	1.5

from low values of 0.59 mg L^{-1} from site 3 (a medium-sized buffer) during September to a high value of 85.0 mg L^{-1} from site 9 (a small-sized buffer) during May (Table 2). Total nitrogen values of 11.0 and 20.0 mg L^{-1} were recorded in May and June from site 8 (a large-sized buffer) which was burnt in May. Concentrations at site 8 were lower in subsequent months, presumably because the regenerating understorey was taking up water and nutrients and the release of nutrients due to the fire had diminished.

Mean values of total nitrogen from the three different-sized buffer zones and the lake are shown in Table 2. On most occasions, total nitrogen concentration was substantially greater in the flow from the buffer zones compared with the lake water. Statistical analysis showed the total nitrogen concentration measured in water from the small buffer zones was significantly greater (ANOVA, $P < 0.05$) than the medium and large buffer zones (Table 3).

Total phosphorus level was low, with highest concentrations measured from small buffer zones during September. The concentration of total phosphorus in the lake was 0.01 mg L^{-1} on all occasions with the exception of August and September, when the values were less than detection limits (Table 4). The mean values of total phosphorus from the small buffer zones were about three to four times levels measured in the other buffer zones. There were no statistically significant differences (Table 5).

Table 3

One-way ANOVA for total nitrogen concentrations for water originating from the three different-sized buffer zones. Data were transformed by a log function, which was the closest approximation (*cf* untransformed, square-root) to homoscedasticity, Cochran's $C = 0.606$.

Source	df	MS	F	P
Buffer size	2	4.54	3.73	<0.05
Residual	39	1.22		

Results of Tukey's tests on transformed data. Untransformed means (total [N] in mg L^{-1}) are presented in parentheses.

Buffer Size	Small	>	Medium	=	Large
	(12.07)		(3.18)		(6.34)

Table 4

Mean (SEM) levels of total phosphorus (in mg L⁻¹) from the three different buffer sizes and from Lake Clifton during the six sampling periods. Sampling size for the small and medium buffers, $n = 3$ on each occasion. One sample was collected from the lake and from a large buffer zone (site 8) on each occasion.

MONTH	SMALL	MEDIUM	LARGE	LAKE
MAY	0.03 (0.01)	0.02 (0.00)	0.02	0.01
JUN	0.06 (0.02)	0.02 (0.01)	0.16	0.01
JUL	0.06 (0.04)	0.11 (0.05)	0.04	0.01
AUG	0.22 (0.10)	0.06 (0.02)	0.01	<0.01
SEP	0.52 (0.44)	0.02 (0.01)	0.06	<0.01
OCT	0.07 (0.05)	0.03 (0.01)	0.15	0.01

Table 5

One-way ANOVA for total phosphorus concentrations for water originating from the three different-sized buffer zones. Data were transformed by a log function, which was the closest approximation (*cf* untransformed, square-root) to homoscedasticity, Cochran's $C=0.436$.

Source	df	MS	F	P
Buffer size	2	2.46	2.27	NS
Residual	39	1.08		

Extractable nutrient components

Analyses of extractable nutrients showed nitrate and ammonia concentrations were always a small component of total nitrogen concentrations (Table 6). In all measurements, orthophosphate was below detection limits. Concentrations of each nutrient in the lake and in surface flows were similar except for nitrate in July and October when values in the surface flows were 5.5 and 7.5 times those of the lake water respectively.

Table 6

Levels of extractable nutrients (in mg L⁻¹) from the lake and from surface flows during each sampling occasion. Note, values for surface flows are means (SEM), $n = 3$ and lake values are from single samples taken on each occasion.

	LAKE			SURFACE FLOWS		
	NO ₃ ⁻	NH ₄ ⁺	PO ₄ ³⁻	NO ₃ ⁻	NH ₄ ⁺	PO ₄ ³⁻
MAY	0.10	0.18	<0.01	0.11 (0.03)	0.53 (0.34)	<0.01
JUN	0.02	0.10	<0.01	0.01 (0.01)	0.02 (0.02)	<0.01
JUL	0.02	0.02	<0.01	0.11 (0.01)	0.05 (0.03)	<0.01
AUG	0.04	0.05	<0.01	0.04 (0.00)	0.05 (0.00)	<0.01
SEP	0.07	0.02	<0.01	0.05 (0.02)	0.03 (0.01)	<0.01
OCT	0.04	0.03	<0.01	0.29 (0.14)	0.02 (0.00)	<0.01

Discussion

Our results showed the inadequacy of the existing small buffer zones on the eastern catchment of Lake Clifton to control nutrient inputs. Both surface water

discharge and the nutrient concentration of the water from the small buffer zones were substantially greater than from the other zones measured. The inadequacy of the small zones and the impact of surface flow into the lake is mitigated, in part, by the low volumes of water flowing from the buffer zones. Measured surface discharge from all nine buffer zone sites accounts for a small amount of the total volume of Lake Clifton. However, total rainfall in Yalgorup National Park during 1993 was significantly less than average. During wetter years, surface flow is expected to make a greater contribution to the water level of the lake.

A previous fire in a large buffer zone probably resulted in substantial nutrient inputs into the lake. This declined over the next few months, presumably as re-vegetation of the understorey buffer zone increased, reducing both water and associated nutrient levels. The concentrations of phosphorus and nitrogen in streams in northwestern United States increased after a wildfire from 5 to 60 fold over background levels (Spencer & Hauer 1991). Fortunately, fires are probably relatively infrequent in buffer zones around most wetlands of the Swan Coastal Plain, although management practices need to recognise the effects of nutrient release after fires around both lakes and streams.

The total nitrogen content of surface runoff from the small buffer zones was significantly greater than for the other buffer zones. Similarly, total phosphorus concentration in the smaller buffers was about 4 times the concentration from the other buffers. Nutrient concentrations in surface water were high compared with groundwater levels (*e.g.* Moore & Turner 1988). The mean nutrient concentrations in pore water were: total phosphorus 0.03 mg L⁻¹; total nitrogen 0.05 mg L⁻¹; ammonium 0.05 mg L⁻¹ and nitrate 0.02 mg L⁻¹ (Moore & Turner 1988). Concentrations of total phosphorus and nitrate in pore water were similar to the lowest values recorded in surface water while total nitrogen was two orders of magnitude lower in groundwater than surface water.

Many of the wetlands of the Swan Coastal Plain receive high levels of nutrients from their surrounding catchments and are becoming increasingly eutrophic. The following factors contribute to the increased rates of eutrophication (Birch 1984; Yeates *et al.* 1985; Schofield *et al.* 1985; Sanders *et al.* 1988; Humphries & Bott 1988): limited nutrient-holding capacity of the sandy Coastal Plain soils; a high and seasonal rainfall; the shallow water-table; extensive drainage of waterlogged soils; the over-use of fertilisers; inadequate treatment of effluent and inappropriate drains into wetlands.

Nutrient enrichment of wetlands may be reduced by adequate buffer zones; however, in the absence of scientific information, arguments for larger buffer zones have had little influence (Lane 1991). This study provides the first empirical data on the capacity of buffer zones to reduce nutrient input into wetlands of the Swan Coastal Plain and complements research elsewhere (*e.g.* Doyle *et al.* 1977; Overcash *et al.* 1981). Based on the results from nutrient enrichment of Lake Clifton, an adequate buffer zone would be considered to be greater than the "medium" buffer width (100-150 m) category of this study. Davies & Lane (1995) recommend a buffer zone of at least 200 m to minimise nutrient enrichment of wetlands

on sandy soils. That recommended width is supported by the results of this study.

Many pools formed in depressions on the shoreline became continuous with the main body of the lake water during late winter. Some of these pools, particularly those adjacent to the rural lots with small buffer zones, would result in the input of nutrients into the lake. Future research should measure the nutrient levels in these pools and determine the contribution they make to the total lake nutrient concentrations.

At this stage, Lake Clifton could be classified, on the basis of trophic status (*sensu* Wetzel 1975), as meso-eutrophic. As the surface run-off from the small buffer regions was eutrophic to hyper-eutrophic, future developments need to provide wider buffers to reduce the rate of eutrophication of the lake.

Acknowledgments: We thank the Water Authority of Western Australia (J Kite and L Moore); the Department of Conservation and Land Management (S Dutton); the Royal Aero Club of Western Australia; the Chemistry Centre of Western Australia (R Schulz); and particularly for field assistance, I Craig. Financial support from the Land and Water Resources Research and Development Corporation through the National Riparian Program is acknowledged.

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A new species of *Lerista* (Lacertilia: Scincidae) from Western Australia, *Lerista eupoda*

L A Smith

Western Australian Museum, Francis Street, Perth WA 6000

Manuscript received September 1995; accepted March 1996

Abstract

The new species of skink, *Lerista eupoda*, described here is most like *Lerista gerrardii*, from which it differs in having more digits (two fingers and three toes rather than one finger and two toes) and more supraciliaries (usually five rather than four). *Lerista eupoda* is confined to the semi-arid interior of Western Australia.

Introduction

The late GM Storr's last seven taxonomic papers dealt with the speciose skink genus *Lerista*. Two of these papers reviewed the *macropisthopus* species-group (Storr 1991a, 1991b). Together, they revised all of the taxa assigned to the group except *Lerista gerrardii*, which was presumably omitted because the accession of many more specimens since the previous revision (Storr 1972) had done little to change the concept of *gerrardii*. The new species described here was brought to Storr's attention by G Harold who collected three specimens near Cue, Western Australia. The subsequent collection of more specimens, which are all consistent in their digital formula, indicates they represent an undescribed taxon.

None of the ten species of *Lerista* already described from Western Australia, that have a digital formula of 2+3, approach the new species in terms of their gross morphology or colour pattern. *Lerista borealis*, *L. bunglebungle* and *L. walkeri* are endemic to the Kimberley region, and have dorsal patterns reduced to rows of dots; *L. planiventralis* is a highly specialised, sharp-snouted burrower with an acute ventrolateral flange, paravertebral rows of dots and a dorsolateral stripe; *L. lineata* has a fixed eyelid, paravertebral lines, a dorsolateral stripe and only 16 midbody scale rows; and *L. allochira* is a small (up to 37mm SVL), almost patternless species, allied to *L. muelleri*.

The remaining species, *Lerista axillaris*, *L. desertorum*, *L. puncticauda* and *L. macropisthopus* occur in the arid and semi-arid regions of southern Western Australia. None of these species has a solid vertebral stripe like the new species; in fact, *L. macropisthopus*, the only species that has a digital formula of 2+3 and is sympatric with the new species, is patternless.

The new species is compared with *Lerista gerrardii*. Although *L. gerrardii* has fewer fingers and toes (1+2, sometimes 0+2), their dorsal patterns are identical. That the new species has a distribution that is almost sympatric with *L. gerrardii* suggests that it is a new species rather than a subspecies.

Notation used by Storr (1984, 1991a) to score supraciliary fusions is adopted here to describe certain

conditions in *L. eupoda* and *L. gerrardii*. The various degrees of fusion are as follows; second supraciliary fused with first supraocular (1+3); first and second supraciliary fused with first supraocular (0+3); first supraciliary fused with first supraocular (0+4); second supraciliary fused with first supraocular, third and fourth supraciliary fused (1+2); first and second supraciliary fused to first supraocular, third and fourth supraciliaries fused (0+2); second supraciliary fused with first supraocular and a very small extra supraciliary posterior to fused scales (1+4).

All specimens examined are housed in the Western Australian Museum.

Systematics

Lerista eupoda sp. nov.

Holotype

R103943, a male in Western Australian Museum, collected by G Harold on 15 February 1990 at 14 km NNE Cue, Western Australia, at 27°19'S, 117°57'E.

Paratypes

North-west Division (WA); 16 km NNE Cue (103944); 35 km SSW Meekatharra (108853-54); 70 km NNE Cue (104363, 120153-54); Telegoothra Hill (87814).

Diagnosis

Distinguished from *Lerista gerrardii*, which has 1 finger (sometimes a stump) and 2 toes, and rarely more than 4 supraciliaries, by having 2 fingers, 3 toes and mostly 5 supraciliaries, and from *Lerista desertorum* by having more supraciliaries and a solid blackish-brown vertebral stripe (*desertorum* usually has 0+3, very rarely five supraciliaries, and a paravertebral series of brownish dots).

Description

Snout-vent length 40-87 mm; sexed males 60-87 mm (n=5), females 56-77 mm (n=2). Length of appendages (% of SVL): forelimb 3.4-5.0%, hindlimb 13.0-17.5%, snout to forelimb 23-25%. Eyelid moveable.

Nasals narrowly separated (n=6) or in contact (n=2). Prefrontals widely separated. Frontoparietals narrowly

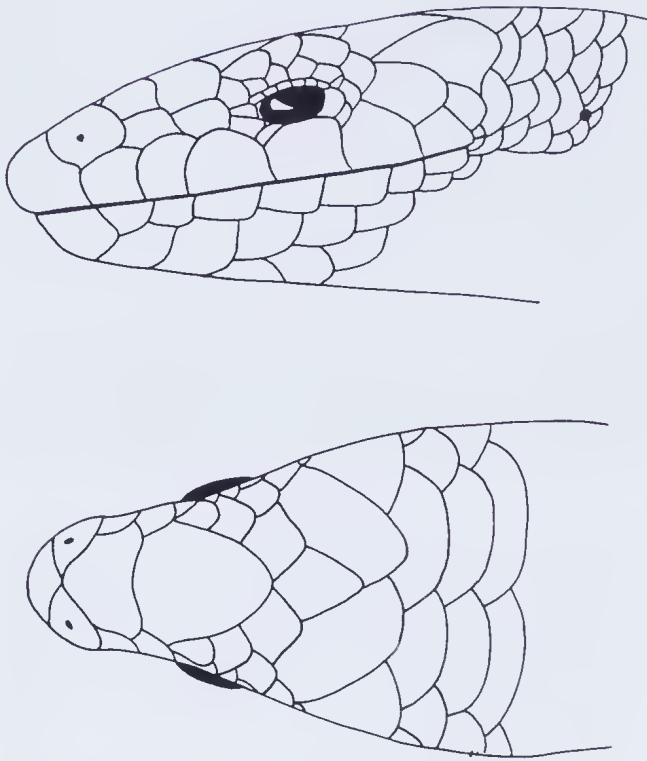


Figure 1. Head of holotype of *Lerista eupoda* (R103943).

separated, smaller than interparietal. Nuchals 2 or 3. Supraoculars 3, first 2 in contact with frontal. Supraciliaries 5 (1+3 one specimen), second and last smallest. Upper labials 6. Three temporals, upper secondary much the largest, lower secondary much the smallest (see Figure 1). Midbody scale rows 20. Paravertebrals; males 82-92 ($n=5$, mean 84.0), females 89-91 ($n=2$, mean 90.0). Lamellae under longest toe 11-16.

Upper surfaces brownish-white or very pale brown. Broad brownish-black vertebral stripe (more than one scale wide) from nape to base of tail, after which it breaks up into two series of angular blackish-brown spots. Broad brownish-black upper lateral stripe (nearly two scales wide) from nasal to base of tail, after which it

breaks up into three series of angular blackish-brown spots or a series of narrow, curving vertical bars. Upper surfaces of limbs stippled blackish-brown. Lower surfaces whitish (see Fig 2).

Distribution

Only known from the arid southern interior between Cue and Meekatharra (Fig 3).

Habitat

Open mulga on red loams and sandy loams.

Comparison with other species

Despite the fact that two of the other seven members of the *Lerista macropisthopus* species-group with two fingers and three toes (*L. macropisthopus macropisthopus* and *desertorum*) are sympatric or geographically close to the new species (Storr 1991a), it is more pertinent to compare it with *L. gerrardii*. Digital formulae aside, the details of colour pattern for *eupoda* are almost identical to *gerrardii*. This, together with the observation that *L. gerrardii* and *L. eupoda* are probably sympatric NW of Cue (Woolgorong Rock where *L. gerrardii* has been collected, is only about 20 km SW of Telegoothra Hill, the most south-westerly locality for *L. eupoda*) led to the comparison of *eupoda* with a series of 72 *L. gerrardii* specimens (see specimens examined).

As is the case for other members of the *L. macropisthopus* species-group, fusion of supraciliaries with supraoculars occurs in *L. gerrardii*. Most of the supraciliary-supraocular fusions involve the first supraocular and the first and second supraciliary. Fusion of the first supraciliary, first two supraciliaries, and the second supraciliary (0+4, 0+3 and 1+3 respectively) to the first supraocular account for 93% of the variation in the supraciliary series in *L. gerrardii*, which without fusions, would have to complete series of five supraciliaries. The remaining seven percent of variation is caused by the occasional fusion of the third and fourth supraciliary (0+2, 1+2) or, in rare cases, the splitting of a supraciliary (1+4).

Proportions of various conditions of fusion in *L. gerrardii* were as follows (where possible condition of both sides of each specimen scored); 1+3 ($n=53$); 0+3



Figure 2. *Lerista eupoda* specimen R104363 (photograph by B Maryan).

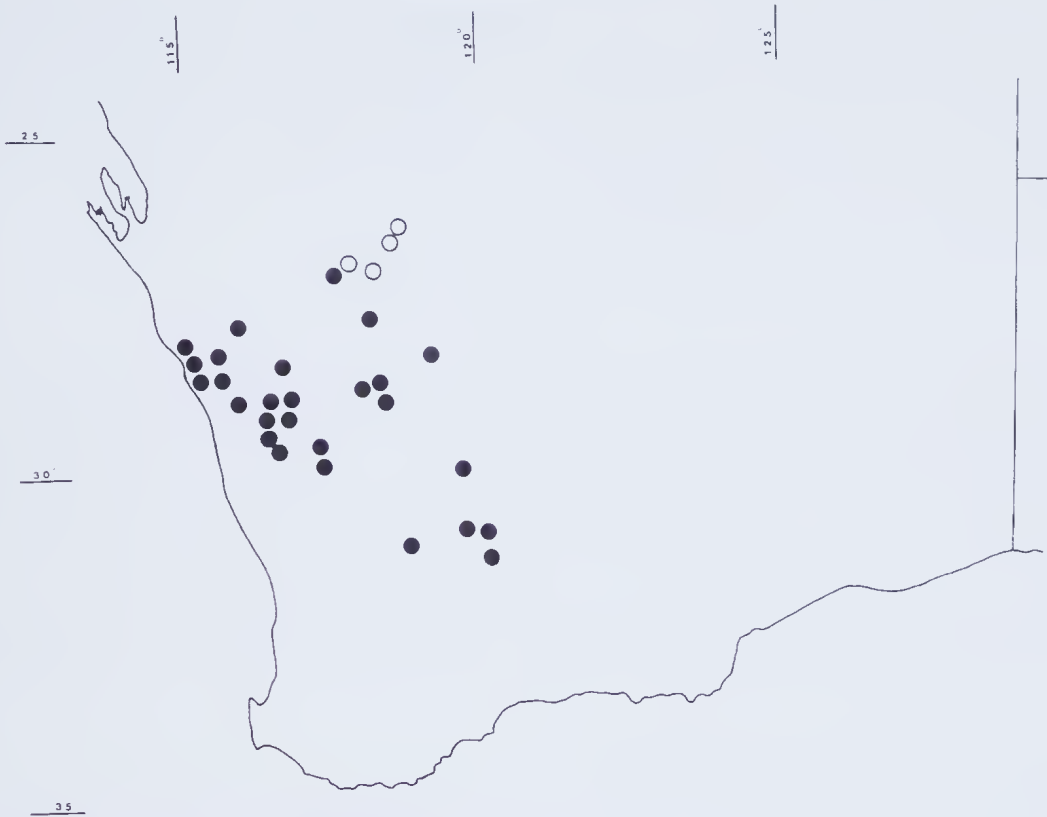


Figure 3. Map showing the distribution of *Lerista gerrardii* (●) and *Lerista eupoda* (○).

($n=34$); 0+2 ($n=3$); 1+2 ($n=3$); 0+4 ($n=3$); 1+4 ($n=1$). The supraciliary configuration for 13 (19%) of specimens was different on either side of the head; the combinations included 1+3, 5 (5 specimens); 1+3, 1+2 (2 specimens); 0+3, 1+2 (2 specimens); 0+3, 0+2 (1 specimen); 0+3, 1+3 (1 specimen); 0+3, 1+4 (1 specimen); 1+3, 0+4 (1 specimen).

Snout-vent lengths of male *L. gerrardii* ranged from 36–80 mm ($n=25$, mean 70.2), females 56–91 mm ($n=29$, mean 76.7 mm). Paravertebral counts for males ranged from 75–102 ($n=22$, mean 90.5), females 83–107 ($n=24$, mean 92.2).

The distributions of *L. eupoda* and *L. gerrardii* abut and it could be argued that the distinguishing characters of *L. eupoda* are only part of the variation of *L. gerrardii*. If having extra digits was all that characterised *L. eupoda* then this could be the case, but the localised shift in digital formula is matched, almost exactly, in a shift in the proportion of specimens with a complete series of supraciliaries (87% in *L. eupoda*, 5% in *L. gerrardii*). Furthermore, the digital and supraciliary variation present in *L. gerrardii* is scattered and not concentrated in the northeast where it would be expected were there intergradation between the two taxa. The only specimen of *L. gerrardii* with two uninterrupted series of supraciliaries (5+5) is from Georgina; the five specimens of *gerrardii* with a series of five supraciliaries on one side are from widely scattered localities such as the Northampton district, Pindabunna and Toomey Hills while specimens with fingers reduced to a stump came from Northampton, Wubin, Jibberding and Southern Cross.

Specimens examined

North-west Division (WA): Walganna Rock (95290);

Woolgerong Rock (97028–29); 15 km N Mt Magnet (88801–02); 40 km NE Paynes Find (83187, 83204–206); 30 km NNE Paynes Find (108855); 19 km NNE Paynes Find (117306); 11 km NNE Paynes Find (84145); 10 km NNE Paynes Find (91133); 10 km NNE Pindabunna (83802, 83805–06).

South-west Division (WA): 8 km W Tallering Peak (115068–69); 5 km N Northampton (115866); Northampton (176, 25960, 31973–74, 66193–94, 71047, 73102–03); Naraling (119168–70); Howetharra Hill (95864); East Chapman (4430); Chapman Valley Research Station (49947–49950); Newmarracarra (1729, 3847); Geraldton (8597); 10 km S Mugga Mugga Hill (98161–98164); Moonyanooka (53693); 5 km ESE Mt Kenneth (108295); Georgina (114681); Mingenew (34103); Lochada (96628); Morowa (39160); 29 km SW Morawa (56831); Perenjori (943); 45 km NE Wubin (113567–68); 66 km NE Wubin (11004); 13 km NE Jibberding White Well (28263); Jibberding (81629); Winchester (3847); Coorow (6941, 10145); Maya (27914); 26 km NE Dalwallinu (58176); Merredin (7351).

Eastern Division: 7.5 km E Yuinmery HS (66052, 66059); 13 km NE Bungalbin Hill (94485); 16 km SSW Mt Jackson (hill) (76105); Southern Cross (34577); Yellowdine (97758); 15 km E Toomey Hills (78795, 78805); 15.5 km S Toomey Hills (71841); Toomey Hills (117372).

Etymology

From Greek *eu* (well) + *pod* (foot). An allusion to the extra digits (compared to *L. gerrardii*).

Acknowledgments: I am grateful to Brad Maryan for the photograph of specimen R104363 and to RE Johnstone for assistance with figures.

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Biogeography of the herpetofauna of the Archipelago of the Recherche, Western Australia

L A Smith & R E Johnstone

Western Australian Museum, Perth WA 6000

Manuscript received September 1995; accepted April 1996

Abstract

Published and unpublished herpetological data collected up until 1995 are collated for 47 islands in the Archipelago of the Recherche, off the south coast of Western Australia. The 20 species of reptile and one species of frog found on the Archipelago's islands represent only 42% of the herpetofaunal diversity of the Esperance Plain on the adjacent mainland. The six most common and widely distributed species are the geckos *Phyllodactylus marmoratus marmoratus* and *Underwoodisaurus milii*, and the skinks *Ctenotus labillardieri*, *Egernia kingii*, *E. napoleonis* and *Hemiergis peronii*. The herpetofauna of individual islands ranges from just one of these common species on the smallest islands, to 16 species (including all of the core suite of common species listed above) on the largest island. The snake, *Pseudonaja affinis tanneri* is the only reptile endemic to the Archipelago. A similarity index based on average linkages (UPGMA) indicates that the Archipelago's herpetofauna is most similar to that of the eastern end of the Esperance Plain.

Introduction

The islands of the Archipelago of the Recherche off the southern Western Australian coast (Fig 1) lie between longitudes 120°30'S and 124°10'E and up to 60km offshore in the west (Termination Island in 35°28'S, 121°59'E) and 30km offshore to the east (Daw Island in 33°51'S, 124°06'E). There are about 200 islands in the Archipelago, ranging in size from over 1000 ha (Middle Island, having most vegetation types and most plant species) to many small islands less than 10ha that have little vegetation or are no more than exposed rocks. The Archipelago, with the exception of High, Station and Woody islands, was vested in the Western Australian Wildlife Authority as an A class reserve on 19 April, 1980.

European knowledge of the natural history of these islands began nearly 200 years ago with the investigations of Labillardière and Riche on the "Recherche" and "Esperance" under the command of d'Entrecasteaux. Matthew Flinders charted the islands in 1802 and Captain Phillip Parker King of the Royal Navy made a short visit in 1818. The remainder of the nineteenth century saw the Archipelago exploited by sealers and pastoralists, the latter with minimal success. The little biological data collected during this time was anecdotal and imprecise (Bechervaise 1954).

The beginning of the twentieth century saw the first attempt to systematically investigate the natural history of the islands. JT Tunney, the Western Australian Museum's professional collector at the turn of the century, made mammal and bird collections from some of the largest islands in 1904 and 1906 (Whittell 1954). This was followed by an expedition in 1921 which included Messrs Hull, Wright and Grant (Hull 1922). DL Serventy made visits in 1944 (Serventy 1947) and again in 1947 and 1948 (Serventy 1952). In 1950, an expedition organised by the Australian Geographical Society sys-

tematically worked its way through the Archipelago, visiting 20 islands (Fairbridge & Serventy 1954; Glauert 1954 & Willis 1953). More recently, naturalists such as Abbott & Black (1978), Goodsell *et al.* (1976), Lane (1982a,b,c), Lane & Daw (1985), Maryan & Robinson (1987) and Tingay & Tingay (1982a,b) have published on collections and observations on the reptiles of the Archipelago. Other contributors, including AA Burbidge, I Cook, J Dell, A Hopkins, D Knowles, NL McKenzie, D Pearson & A Williams, VN Serventy, AN Start and A Weston, have lodged specimens and unpublished observations with the Western Australian Museum. Since 1979, we have had the opportunity of visiting many more islands to collect birds and reptiles. Despite all efforts, Storr (1987) lists bird data from only about 50 islands, while Western Australian Museum records together with published observations give herpetological data for only 47 islands.

The aim of this paper is to collate and review the scattered published and unpublished herpetological data available for the Archipelago of the Recherche, and to compare it with the herpetofauna of the opposite mainland.

Results

The particular species that have been recorded on the various islands of the Recherche Archipelago are listed in Appendix 1 and summarised in Table 1. Recent collecting has thrown doubt on some earlier observations; these earlier and doubtful observations, and certain unidentifiable published descriptions of reptiles from particular islands, are excluded from this list.

Substantial efforts by a number of collectors have not confirmed the sight record of *E. kingii* from Daw Island (Glauert 1954). Specimens of *Egernia napoleonis* from the south coast of Western Australia, east of Bremer Bay (including the Archipelago of the Recherche), are larger than specimens from Western populations (Storr 1978). Specimens of *E. napoleonis* from Daw Island are excep-

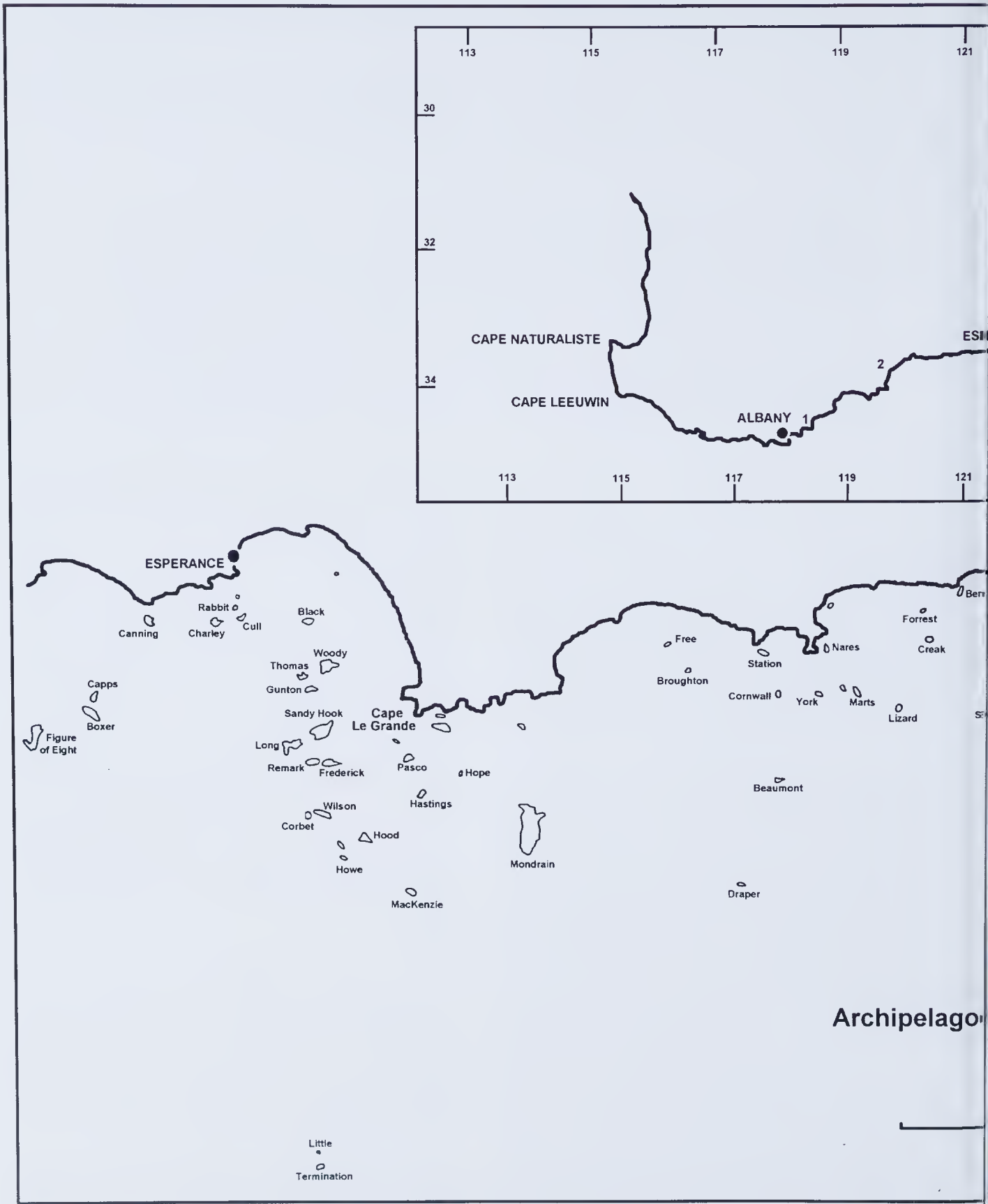
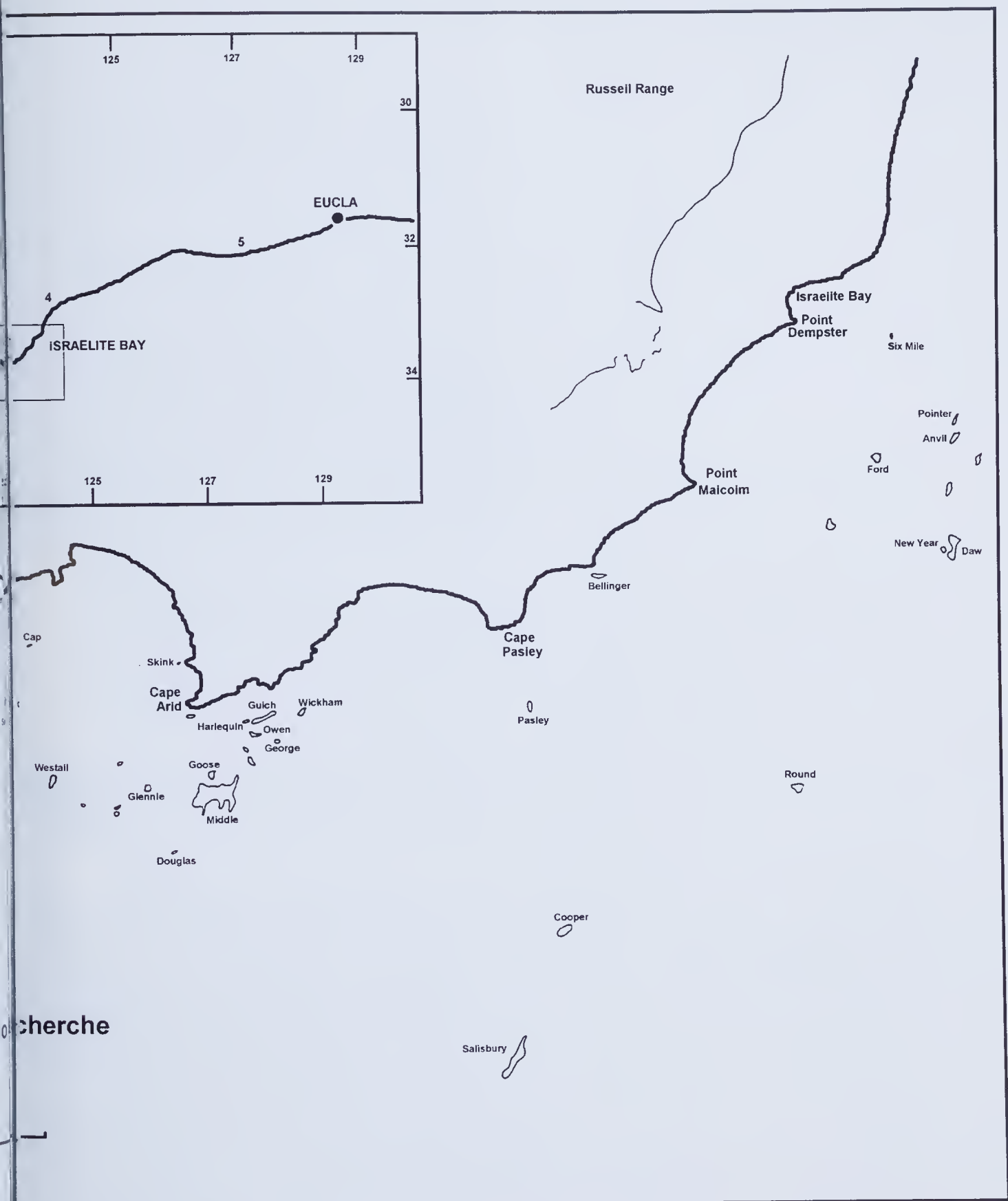


Figure 1. The Archipelago of the Recherche, showing major islands mentioned in the text and; inset, the location of 5 mainland areas with w plain below Wylie Escarpment (4), Roe Plain (5).



una of the Archipelago of the Recherche is compared; Two Peoples Bay (1), Fitzgerald River National Park (2), Cape Le Grand National Park (3),

Table 1

The number of islands which have one species, two species, and so on, up to 16 species supported by the largest island. The area of the largest island, within a suite of islands supporting the same number of species, is also given.

Number of species	Number of islands	Area of largest island (ha)
1	7	100
2	8	140
3	6	130
4	7	100
5	9	280
6	3	285
7	2	190
8	1	125
9	1	315
10	0	-
11	1	300
12	0	-
13	0	-
14	0	-
15	1	780
16	1	1080

tionally large (up to 145 mm SVL and 94 grams) so it is possible that Glauert's observation is based on these large *E. napoleonis*.

Despite extensive work on Mondrain Island by Abbott & Black (1976), Johnstone (unpublished observations) and Pearson & Williams (*pers. comm.*), there has not been a specimen of *Hemiergis peronii* to substantiate a sight record (Glauert 1954). It is possible that Glauert's sight record is based on *Lerista dorsalis*, because *H. peronii* and *L. dorsalis* have the same digital formula (4+4) and many *H. peronii* from the Archipelago develop dorsal stripes similar to those of *L. dorsalis*.

Names of some lizards have changed since the publication of earlier lists. The skink *Lerista dorsalis* is the *Lerista frosti* of Abbott & Black (1978) and the *Ablepharus elegans* of Glauert (1954). *Gemmatophora norrisi* is the *Amphibolurus muricatus* of Abbott & Black (1978).

The names of some islands have also changed. In the past, MacKenzie Island (34°12'S, 122°06'E) has been called Round Island; Westall Island (34°05'S, 122°58'E) has been called Combe Island; Cull Island (33°55'S, 121°54'E) has been called Gull Island; Kermadec Island (34°05'S, 122°05'E) has been called Wedge Island; Wickham Island (34°01'S, 123°17'E) has been called Stanley Island; and Daw Island (33°51'S, 124°06'E) has been called Christmas Island. Anvil Island (33°44'S, 124°05'E), Skink Island (33°59'S, 123°09'E), Harlequin Island (34°01'S, 123°14'E),

Table 2

Habitat of 19 reptile and amphibian taxa in the Archipelago of the Recherche. Numbers in columns indicate the number of individuals found in each habitat.

Species	Habitat	Under shrubs on sand	On or under granite	On or under limestone	On or under leaf litter	On <i>Carpobrotus</i>	Under bark	On beach sand	In burrow in soil	In loose soil
<i>Litoria cyclorhynchus</i>			2							
<i>Phyllodactylus m. marmoratus</i>			75	1	2		1			
<i>Underwoodisaurus milii</i>			29	2						
<i>Ctenophorus ornatus</i>			29							
<i>Gemmatophora norrisi</i>				4						
<i>Cryptoblepharus virgatus clarus</i>			1							
<i>Ctenotus labillardieri</i>			65							
<i>Egernia kingii</i>			18	1					1	
<i>Egernia multiscutata bos</i>			2						8	1
<i>Egernia napoleonis</i>	2		80	1					1	
<i>Hemiergis peronii</i>			9					1		6
<i>Bassiana trilineata</i>			3	5						
<i>Morethia obscura</i>			1							
<i>Lerista microtis intermedia</i>								1		
<i>Tiliqua rugosa rugosa</i>			2							
<i>Varanus rosenbergi</i>					1					
<i>Morelia spilota imbricata</i>			1			1				
<i>Acanthophis antarcticus</i>	2									
<i>Notechis coronatus</i>			10		2	1				

Hull Island (33°58'S, 122°50'E, Six Mile Island (33°38'S, 123°57'E) and Tunney Island (33°58'S, 122°49'E) have only recently been named.

Discussion

Species distribution within the Recherche Archipelago

Less than half of the islands in the Recherche Archipelago have reptiles or frogs collected from them, and the collecting effort varies from many days in the case of the larger islands to only an hour or so for the smaller islands. Such incomplete data only allows the most general of conclusions regarding the distribution of species within the Archipelago and species diversity-island area relationships to be drawn.

Table 1, which summarises the data in Appendix 1, shows the number of islands which have one species, two species and so on up to 16 species, and the area of the largest island within a suite of islands supporting the same number of species. The most widely distributed species in the Archipelago, the gecko *Phyllodactylus marmoratus marmoratus*, occurs on 32 islands. It is followed by various skinks; *Egernia kingii* (31), *Egernia napoleonis* (30), *Ctenotus labillardieri* (21), and the gecko *Underwoodisaurus milii* (19) and the skink *Hemiergis peronii* (19). We consider these six species to comprise the "core" herpetofauna of the Archipelago. The most common and widely distributed snake (*Notechis coronatus*) is found on nine islands. *Morelia spilota imbricata* and *Pseudonaja affinis tanneri* are the least common snakes, with the python only occurring on the two largest islands (Middle and Mondrain), and the endemic *P. affinis tanneri* only on Boxer and Figure of Eight Islands, at the western end of the Archipelago. The skink *Lerista microtis intermedia* is restricted to the predominantly sandy Wickham Island, while the monitor *Varanus rosenbergi* is only found on Middle Island.

The four largest islands, of Middle (1080 ha), Mondrain (780 ha), Salisbury (315 ha) and North Twin Peak (300 ha), support 16, 15, 9 and 11 species respec-

tively, and all of them except Salisbury has a complete suite of the six core species. Fewer species utilise the habitats created by limestone than by granites (Table 2), which may explain why Salisbury Island, which is largely Quaternary eolianite (Bechervaise 1954), supports the fewest species of the four largest islands. The remaining 43 smaller islands are less than 300 ha and support only up to eight species.

Comparison with mainland herpetofauna

Lack of data may preclude a thorough analysis of the intra-island herpetofauna for the Archipelago of the Recherche but it does not hinder a biogeographic comparison with the opposite mainland because the herpetofauna assemblages of both areas should now be nearly completely known. Although many small islands in the Archipelago remain unvisited, they probably only support a few of the common species (most likely some, but not all, of the six core suite of species). It is unlikely that few, if any, amphibian or reptile species remain to be added to the 21 species so far recorded from the Archipelago.

Details of the lower west and south coast mainland herpetofauna have been obtained from studies of the coastal strip between Busselton and Two Peoples Bay (How *et al.* 1987), Cape Le Grand National Park (Kitchener *et al.* 1975) and the Great Australian Bight (Storr *et al.* 1981; Congreve 1985; McKenzie & Robinson 1987; Greer *et al.* 1991). These data, which are summarised in Table 3 and augmented with data from Western Australian Museum records pertaining to the plain below Wylie Escarpment (see Figure 1), indicate that the coastal strip from Augusta to Eucla supports a moderately rich herpetofauna.

The herpetology of the long coastal strip between Two Peoples Bay and Roe Plains, to which we have compared the herpetofauna of the Archipelago of the Recherche (Table 4), transects several ecophysical zones. Two Peoples Bay, the westernmost site, is by far the wettest (*ca.* 850 mm rainfall *p.a.*) and represents the southeastern extremity of the jarrah-marri woodlands that is generally

Table 3

The number of species and subspecies recorded from the Archipelago of the Recherche and 5 regions of the adjacent south coast mainland. Numbers in brackets refer to site numbers (Appendix 2).

FAMILY	Two Peoples Bay (1)	Fitzgerald River National Park (2)	Cape Le Grand National Park (3)	Recherche Archipelago	Below Wylie Escarpment (4)	Roe Plain (5)
Leptodactylidae	7	9	4	0	2	0
Hylidae	2	2	2	1	1	0
Cheluidae	1	1	0	0	0	0
Gekkonidae	2	5	3	2	5	5
Pygopodidae	3	5	3	0	2	1
Agamidae	0	2	3	2	3	7
Scincidae	14	14	14	11	17	12
Varanidae	1	0	1	1	1	0
Typhlopidae	0	1	1	0	0	0
Boidae	1	0	1	1	0	1
Elapidae	6	5	4	3	4	3
TOTAL	37	44	36	21	35	29

associated with leached sands over ironstone gravels (Beard 1990). Two Peoples Bay is the eastern limit of southwestern Australian reptile endemics, such as *Egernia luctuosa*, *E. pulchra* and *Glaphyromorphus australis*.

The mainland sites of Fitzgerald River National Park, Cape Le Grand National Park and the plain below Wylie Escarpment are situated on the Esperance Plain which generally becomes more arid with increasing longitude. Ravensthorpe has a mean average rainfall of 420 mm, Esperance 740 mm and Israelite Bay 388 mm (*pers. comm.*, Western Australian Bureau of Meteorology). This undulating plain with scrub heaths and occasional thickets of eucalypts is relieved by numerous granitic and gneissic hills and domes. Most prominent of these is the Barren Range (Fitzgerald River National Park), Mt Le Grand and Frenchman Peak (Cape Le Grand National Park) and Russell Range (plateau above Wyle Escarpment). Israelite Bay is the eastern limit of granitic outcrops. Offshore, where the Esperance Plain is submerged, granite domes continue to protrude above sea level and form the islands of the Archipelago of the Recherche. Dortch & Morse (1984) estimate that Middle Island was formed by rising sea levels at least 9,000 and perhaps as much as 11,000 years ago.

Increasing aridity and the lack of granite, one of the more important microhabitats in the southwest of Western Australia, induces major changes to the herpetofauna of the south coast particularly in the eastern portion of the Esperance Plain. The Western Swamp Turtle (*Chelodina oblonga*) has its eastern limit in the Fitzgerald River drainage, while the lack of lithic complexes terminates the distribution of a number of amphibians and reptiles. Cape Le Grand is the eastern limit of *Ctenophorus ornatus* while the lack of soaks and pools generated by granite outcrops limits the number of amphibians found east of Israelite Bay (Table 3). Israelite Bay is also the eastern limit for the Tiger Snake (*Notechis scutatus occidentalis*) and the pygopod *Delma fraseri*. The python *Morelia spilota imbricata* and the skink *Tiliqua occipitalis* have recently been recorded from the vicinity of Eyre (Griffin & Hunt 1993).

The loss of these south-western herpetofaunal elements is compensated by the western intrusion of semi-arid and arid zone reptiles, in particular agamids and *Lerista*, although the species diversity of the latter in no way approaches the diversity exhibited by this genus on the mid-west coast of Western Australia. Three species of agamid and four species of *Lerista* (*Ctenophorus maculatus*, *C. griseus*, *C. pictus*, *Gemmatophora norrisi*, *Lerista dorsalis*, *L. baynesi* and *L. picturata*) are found on the plain below Wylie Escarpment but not further west on the mainland.

Still further northeast along the coast the Roe Plains (Nullarbor Region, Eremian Province, Beard 1990) is even more arid (Eyre 296 mm rainfall *p.a.*) and is isolated by the Baxter Cliffs in the west, the Hampton Plateau in the north and the cliffs at the head of the Great Australian Bight in the east. It is vegetated with areas of chenopod steppe, scattered Myall and copses of mallee on heavier soils and melaleuca and dense mallee on lighter soils. There are also extensive areas of dune with little or no vegetation. The reptiles are represented by two skinks endemic to the Roe Plains (*Ctenotus brooksi euclae* and *Lerista arenicola*) as well as elements of the Nullarbor

herpetofauna not found further southwest (*Morethia adalaidensis* and *Pogona nullarbor*).

A Simpson's similarity index (Biodiversity 1993) based on the taxa listed in Appendix 2 for the mainland sites of Two Peoples Bay, Cape Le Grande and Fitzgerald National Parks, Esperance Plain below Wylie Escarpment and Roe Plains, and the geckos, pygopods, agamids, skinks and elapids in Appendix 1 using average linkages (UPGMA), indicates that the Archipelago's herpetofauna is least like the western and easternmost mainland sites (Two Peoples Bay and Roe Plain respectively) and most similar to the herpetofauna of Cape Le Grand National Park, Fitzgerald River National Park and Wylie Escarpment of the Esperance Plain (Fig 2). What is, perhaps, a little surprising is the close affinity of the Archipelago's herpetofauna with that of the Wylie Escarpment. The analysis could have been influenced by the fact that three of the four largest islands (Middle, Salisbury, North and South Twin Peak), which collectively support about 90% of the Archipelago's herpetofaunal diversity are situated towards the more arid, eastern end of the Archipelago, and as a consequence are likely to be ecophysically and zoologically most similar to the eastern end of the Esperance Plain.

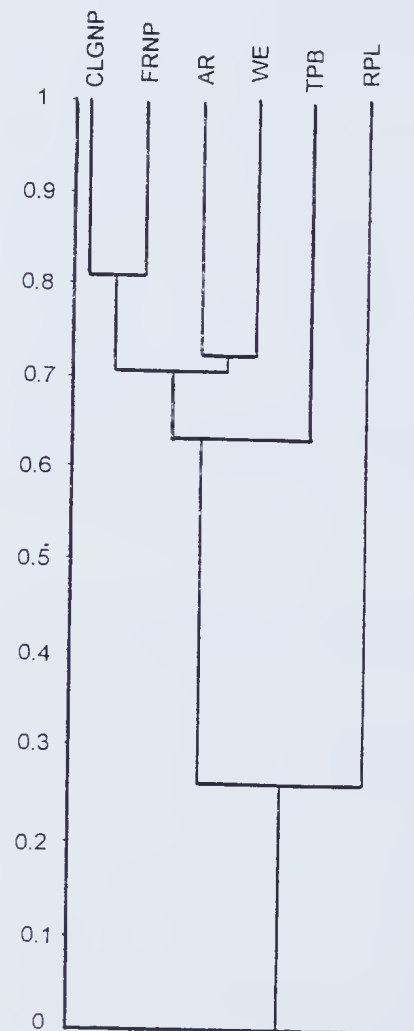


Figure 2. Simpson's similarity index for Archipelago of the Recherche (AR) and the mainland sites, Two Peoples Bay (TPB), Fitzgerald River National Park (FRNP), Cape Le Grand National Park (CLGNP), Wylie Escarpment (WE) and Roe Plain (RP).

With the exception of the endemic race of the dugite (*Pseudonaja affinis tannerii*), the species of amphibians and reptiles on the Archipelago of the Recherche are moderately common to common on the adjacent mainland. In our view, none of these species, including the dugite, require more protection than that currently provided by the 'A' Class Reserve status of the majority of the islands in the Archipelago.

Current South Australian Museum records (A Edwardes, South Australian Museum, *pers. comm.*) indicate that there are now about twice as many species of reptile recorded from the Nuyts Archipelago than indicated by the most recent published paper on the area (Robinson & Smyth 1976). Furthermore, apart from a list of the amphibians and reptiles of Eyre Peninsula (Schwaner *et al.* 1985) there are no published faunal lists for discrete sites on the west coast of South Australia. This lack of recent published data precluded the extension of this study to include island and adjacent mainland amphibian and reptile faunas, east to Eyre Peninsula, South Australia. Nuyts Archipelago is of particular interest because it offers a glimpse of a fauna in an otherwise inundated terrain at the eastern end of the Great Australian Bight. This group of islands mirrors the Archipelago of the Recherche at the western end of the Great Australian Bight.

Acknowledgments: We are grateful to Mr I. Spurr of Israelite Bay for his hospitality and help in getting us to many islands, to Mr and Mrs WH Butler and Mr N Kolichis whose grants helped defray the costs of some of our fieldwork in 1985 and 1986, and Dr RA How (Department of Biogeography and Ecology, Western Australian Museum) for assistance with Figure 2. Ms A Edwardes, South Australian Museum kindly provided us with data on the Nuyts Archipelago. We also thank Mr B Haberley, Department of Conservation and Land Management, Esperance for assistance in 1987 and Mr B Goodchild of Department of Lands and Survey for help with island names.

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Appendix 1. The herpetofauna of the islands of the Archipelago of the Recherche on which species have been found. * indicates specimens in Western Australian Museum; letters indicate observations as follows: a, Australian Geographical Society Expedition (Glauert 1954); b, Lane & Daw (1985); c, Lane (1982a); d, Lane (1982b); e, Lane (1982c); f, Tingay & Tingay (1982a); g, Tingay & Tingay (1982b); h, Maryan & Robinson (1987); i, Goodsell *et al.* (1976); j, Smith & Johnstone (unpublished notes); k, Pearson & Williams (*pers. comm.*).

ISLAND	Approximate area (ha)	<i>Litoria cyclorhynchus</i>	<i>Phyllodactylus m. marmoratus</i>	<i>Underwoodisaurus milii</i>	<i>Ctenophorus ornatus</i>	<i>Gemmatophora norrisi</i>	<i>Cryptoblepharus virgatus clarus</i>	<i>Ctenotus labillardieri</i>	<i>Egernia kingii</i>	<i>Egernia multiscutata bos</i>	<i>Egernia napolconis</i>	<i>Hemiergis peronii</i>	<i>Bassiana trilineata</i>	<i>Morethia obscura</i>	<i>Lerista dorsalis</i>	<i>Lerista microtis intermedia</i>	<i>Tiliqua rugosa rugosa</i>	<i>Varanus rosenbergi</i>	<i>Morelia spilota imbricata</i>	<i>Acanthophis antarcticus</i>	<i>Notechis coronatus</i>	<i>Pseudonaja affinis tanneri</i>	Total number of species
ANVIL	25			j				*		*	*	*											5
BELLINGER	40		*						*	*	*	*											5
BEN	55		*					*	*		*	*											4
BOXER	200							*	a		*	*								*		*	6
CAVE	3		a	*							*	a											4
CHARLEY	100			*				*	a														3
CORBET	100		*		b			*			*												4
CULL	70			*					*		*												3
DAW	180		*	*	*				a		*									*	*		7
DOUGLAS	30				*				a														2
FIG. OF EIGHT	200		*					*	a											a		*	5
FORREST	20		*					*	*		*												4
FREDERICK	80								d														1
GOOSE	85		*					*	*		*										*		5
GULCH	100		*					*	*		*										*		5
GUNTON	95		*						a														2
HARLEQUIN	10		*					*			*												3
HIGH	10							*	*		*	*									*		5
HOOD	130							f	f		f												3
HOPE	25										*												1
HULL	20		*	*							*	*											4
INSHORE	35		*					*	*	*	*												5
KERMADEC	30		a						a														2
LONG	140		a						a														2
MACKENZIE	50								c			c											2
MIDDLE	1080	*	*	*	*	*	*	*	*		*	*	*	*	*	*	*	*	*	*	*	*	16
MONDRAIN	780	*	*	*	*	*	*	*	*		*	a			*		*		*	k	*		15
NEW YEAR	20										*												1
NARES	5		*				*				*												3
N TWIN PEAK	300		*	*			*	*	a		*	*					*		*	*	*		11
S TWIN PEAK	115		*	*					a														3
OWEN	25		*									*											2
PASCO	85		a	a	a				a			a											5
RABBIT	<10		*																				1
REMARK	100		*	a	*				a&e														4
SALISBURY	315		*	*					*	*	*	*	*				*				*		9
SANDY HOOK	285		*	*				g			*	g							a&g				6
SIX MILE	10										*												1
SKINK	10							*	*			*											3
TAYLOR	15		*						a		*	*			*				*				6
TERMINATION	85		*	*				*	a						a								5
THOMAS	100		*	*							*												2
TUNNEY	25		*	*					*		*												4
WESTALL	100										*	*											1
WICKHAM	40										*					*							2
WILSON	125		*	*				*	*		*	*	*	*							*		8
WOODY	190		h&i	h&i			h	h&i			*	h&i		h									7

Appendix 2. Species and subspecies of geckos, pygopods, agamids, skinks and elapid snakes recorded from 5 sites on the south coast mainland adjacent to the Archipelago of the Recherche. Numbers in brackets refer to site numbers (Fig 1).

	Two Peoples Bay (1)	Fitzgerald River National Park (2)	Cape Le Grand National Park (3)	Wylie Escarpment (4)	Roe Plain (5)
Gekkonidae					
<i>Crenadactylus ocellatus ocellatus</i>		*			
<i>Gehyra variegata</i>				*	*
<i>Phyllodactylus marmoratus marmoratus</i>	*	*	*	*	
<i>Phyllodactylus marmoratus alexanderi</i>				*	*
<i>Diplodactylus granariensis</i>	*	*			*
<i>Diplodactylus spinigerus inornatus</i>		*	*	*	*
<i>Underwoodisaurus milii</i>		*	*	*	*
Pygopodidae					
<i>Aprasia inaurita</i>					*
<i>Aprasia repens</i>		*			
<i>Aprasia striolata</i>	*	*	*		
<i>Delma australis</i>	*	*	*		
<i>Delma fraseri fraseri</i>		*		*	
<i>Pygopus lepidopodus lepidopodus</i>	*	*	*	*	
Agamidae					
<i>Ctenophorus maculatus griseus</i>		*		*	*
<i>Ctenophorus ornatus</i>			*		
<i>Ctenophorus pictus</i>					*
<i>Genimatomphora norrisi</i>				*	*
<i>Pogona minor minor</i>			*		*
<i>Pogona nullarbor</i>					*
<i>Tympanocryptis adelaidensis chapmani</i>		*	*	*	*
Scincidae					
<i>Cryptoblepharus virgatus clarus</i>		*			*
<i>Bassiana trilineata</i>	*	*	*	*	
<i>Ctenotus catenifer</i>	*	*	*	*	
<i>Ctenotus gemmula</i>		*	*	*	
<i>Ctenotus labillardieri</i>	*	*	*	*	
<i>Ctenotus impar</i>				*	
<i>Ctenotus brooksi euclae</i>					*
<i>Egernia bos</i>	*	*	*	*	
<i>Egernia kingii</i>	*		*		
<i>Egernia luctuosa</i>	*				
<i>Egernia napoleonis</i>	*	*	*	*	
<i>Egernia pulchra</i>	*				
<i>Glaphyromorphus australis</i>	*				
<i>Hemiergis initialis brookeri</i>		*		*	*
<i>Hemiergis peronii</i>	*	*	*	*	
<i>Lerista baynesi</i>				*	*
<i>Lerista distinguenda</i>		*	*	*	
<i>Lerista microtis microtis</i>	*				
<i>Lerista microtis intermedia</i>		*	*	*	
<i>Lerista dorsalis</i>				*	*
<i>Lerista picturata</i>				*	
<i>Lerista arenicola</i>					*
<i>Menetia greyii</i>		*	*		*
<i>Pseudomoia baudini</i>					*
<i>Tiliqua occipitalis</i>	*		*	*	*
<i>Tiliqua rugosa rugosa</i>	*	*	*	*	*
<i>Morethia adelaidensis</i>					*
<i>Morethia obscura</i>	*	*	*	*	*
Elapidae					
<i>Notechis coronatus</i>	*	*	*	*	
<i>Notechis curtus</i>	*	*	*		
<i>Notechis mastersii</i>				*	*
<i>Notechis minor</i>	*				
<i>Notechis scutatus occidentalis</i>	*	*	*	*	
<i>Pseudonaja affinis affinis</i>	*		*	*	*
<i>Rhinoplocephalus bicolor</i>	*	*			
<i>Rhinoplocephalus nigriceps</i>		*			
<i>Rhinoplocephalus spectabilis</i>					*

Population and plant growth studies of six species of *Eremophila* (Myoporaceae) from central Western Australia

G S Richmond¹ & E L Ghisalberti²

¹ School of Environmental Biology, Curtin University of Technology, GPO Box U1987, Perth WA 6001;
present address: BSD Consultants, PO Box 155, Subiaco WA 6008

² Department of Chemistry, The University of Western Australia, Nedlands WA 6907

manuscript received January 1996; accepted July 1996

Abstract

Growth of six *Eremophila* (Myoporaceae) species occurring in central Western Australia were investigated over a period of three years. Field studies at Mt Keith Station (Wiluna) and Mt Weld Station (Laverton) indicated that *Eremophila* showed both germination and growth responses after heavy rainfalls. *Eremophila spectabilis brevis* increased in number from 2407 to 17684 plants ha⁻¹ after a one in fifteen year rainfall event. *Eremophila fraserii galeata* increased from 2650 to 9640 plants ha⁻¹ in the same period. The other species monitored, *E. exilifolia*, *E. forrestii*, *E. latrobei latrobei* and *E. margarethae*, also showed significant population increases. *Eremophila* germination strategies included generation of multiple seedlings as well as staggered germination from the same fruit over a one year period. Seedling survival was as high as 72% for *E. latrobei latrobei* after one year and seedlings reached a mean height of 8.3 cm in this period. Adult plants increased in height and leaf cover even during adverse seasons. A study of the seed bank of an *E. fraserii galeata* community revealed a mean of 56 fruits m⁻² under shrubs compared to 2 fruits m⁻² in bare ground.

Introduction

Eremophila species (Myoporaceae) are hardy perennial shrubs and small trees which occur throughout the arid and semi-arid regions of Australia (Chinnock 1981, 1986), and currently number over 315 species and sub-species (Chinnock *pers. comm.*). The main centre of diversity is the Austin phytogeographic region of Western Australia (Beard 1980). Since many species are tolerant to drought, fire, frost, salinity and grazing, interest in this genus is centred on its potential in rangeland revegetation and minesite rehabilitation programmes (Richmond & Ghisalberti 1994a). There have been number of studies on the taxonomy and biology of *Eremophila* (Beard 1965; Barlow 1971; Bowen 1975; Smith 1975) and their propagation potential (Lothian & Holliday 1964; Beard 1968; Wrigley & Fagg 1979). A detailed examination of the reproductive biology, vegetative and floral morphology of *Eremophila* has also been reported (Chinnock 1982).

Knowledge of the population dynamics of species of this genus is limited. Fruit production and germination in *E. gilesii* and *E. mitchellii* were most noted after rains (>40 mm) during the winter months, March-September (Burrows 1971, 1972; Beeston & Webb 1977). Seed bank studies of *E. gilesii* have demonstrated that the soil can contain more than 400 fruits m⁻². *Eremophila spectabilis* increased to 700 plants ha⁻¹ yr⁻¹ in a grazed paddock during a wet period in 1973-76, and decreased to 116 plants ha⁻¹ yr⁻¹ during a drought period in 1979-82 (Gardiner 1986a,b). *Eremophila delisseri* and *E. maculata* responded favourably to grazing pressure while *E. forrestii* declined in numbers (Hacker 1987). This study describes plant density, seedling recruitment, survival

and growth habits of six species in the Laverton and Wiluna areas of WA over a period of three years.

Methods

The sites selected were at Mt Keith Station (27°17'S, 120°31'E) and Mt Weld Station (28°38'S, 122°24'E) in central Western Australia. An initial survey showed that these sites contain a wide range of *Eremophila* species. From the Mt Weld site, two species were selected for detailed study; *E. forrestii* (MWS1) and *E. margarethae* (MWS3) which are co-dominant species throughout the area located within populations of *Atriplex* (saltbush) and *Maireana* (bluebush) species. From the Mt Keith site, five species were chosen; *E. exilifolia* F. Muell. (MKS1), *E. forrestii* (MKS2), *E. fraserii galeata* Chinnock (MKS3), *E. latrobei latrobei* F. Muell. (MKS4) and *E. spectabilis brevis* Chinnock (MKS5). *Eremophila fraserii galeata* dominates the understorey throughout this area, with *E. spectabilis brevis* as a sub-dominant species. The other three species occur at lower densities and are scattered throughout the region (Speck 1963). General details of the location of the selected species and associated flora are given in Table 1. Adult plant density, seedling recruitment, survivorship, and growth habits were evaluated for each species. The data were collected over the period September 1990-June 1993.

Assessment of seasonal plant growth period

The climate of the two study areas can be described as arid. The average rainfall at Mt Keith and Mt Weld is 218 and 221 mm respectively. Winter rainfall at Mt Keith is due to the passage of westerly frontal systems, while tropical cyclones and thunderstorms account for the precipitation during the summer months. Average monthly rainfall ranges between 4 mm in September to 37 mm in

Table 1

Location and description of selected *Eremophila* species at the two study sites.

Species	Location	Description	Associated flora
Mt Weld Station Site			
	30 km west of Laverton 28°38'S, 122°24'E		
<i>E. forrestii</i> (MWS 1) (Wilcox bush)	Jubilee paddock 28°58'96S, 122°27'22"E	shrub to 2 m, hairy branches, obovate-oblong leaves, tubular flowers	<i>Acacia aneura</i> , <i>E. latrobei</i> , <i>Templetonia egena</i> , <i>Maireana</i> <i>triptera</i> , <i>Leichardia australis</i>
<i>E. margarethae</i> (MWS3) (Sandbank Poverty bush)	Brook paddock 28°52'75"S, 122°25'04"E	gray shrub to 1 m, narrowly linear leaves, mauve flowers	<i>A. aneura</i> , <i>M. triptera</i> , <i>Atriplex</i> <i>nummularia</i> , <i>Ptilotus obovatus</i>
Mt Keith Site			
	90 km south of Wiluna 27°17'S, 120°31'E		
<i>E. exilifolia</i> (MKS1)	Jumps Up paddock 27°16'51"S, 120°27'16"E	shrub to 2 m, resinous branches, pink-violet tubular flowers	<i>A. aneura</i> - <i>A. linopylla</i> , <i>E.</i> <i>latrobei</i> , <i>Calytrix glaucophylla</i> , <i>P. obovatus</i>
<i>E. forrestii</i> (MKS2) (Wilcox bush)	Red paddock 27°18'96"S, 120°33'56"E	shrub to 2 m, ovate to oblong leaves, pale pink flowers	<i>A. aneura</i> , <i>E. latrobei</i> , <i>P.</i> <i>obovatus</i> , <i>Cassia</i> sp.
<i>E. fraserii galeata</i> (MKS3) (Turpentine bush)	Rocky Hills paddock 26°10'82"S, 120°36'20"E	shrub to 3 m, resinous leaves, ovate leaves, red tubular flowers	<i>A. aneura</i> , <i>Cassia</i> sp.
<i>E. latrobei latrobei</i> (MKS4) (Warty fuchsia bush)	Red paddock 27°19'01"S, 120°33'54"E	gray, green shrub to 2.5m, warty branches, linear-oblong leaves	<i>A. aneura</i> , <i>P. obovatus</i> , <i>Cassia</i> sp., <i>Triodia basedowii</i>
<i>E. spectabilis brevis</i> (MKS5) (Showy poverty bush)	Two Tanks paddock 27°13'98"S, 120°36'84"E	shrub to 2 m, resinous branches, linear-lanceolate leaves, purple flowers, dark grey bark	<i>A. aneura</i> , <i>E. foliosissima</i> , <i>Eragrostis eriopoda</i> , <i>Prostantha</i> sp.

March. The highest mean maximum monthly temperature was 37.7 °C in January, and the lowest mean minimum monthly temperature was 5.3 °C in July (Bureau of Meteorology, Perth); evaporation exceeds 5440 mm yr⁻¹. As a consequence of episodic rainfall and high evaporation rates, short growing seasons and frequent droughts are characteristic. Rainfall at Mt Weld is more dependable during the late summer with precipitation being brought about by cyclonic activity. Average monthly rainfall ranges between 7 mm in October to 31 mm in March. The highest mean maximum monthly tempera-

ture was 35.9 °C in January, and the lowest mean monthly minimum temperature was 5.2 °C in July; evaporation exceeds 3473 mm yr⁻¹ (Beard 1974).

Study site design and assessment

Circular study plots (diameter 25 m) were partitioned into 30° sectors in which the exact location of individual plants could be monitored (Lindsey *et al.* 1958; Mueller-Dombois & Ellenberg 1974). The MKS study sites were visited four times a year in the first year (1991), but this was reduced to two per year (December and June) in

Table 2

Monthly rainfall (mm) for the period 1989-1993 recorded at Mt Keith (Mt Keith Station Exploration Camp, Western Mining Corporation) and Mt Weld station (Granny Smith Gold Mine, Placer Pacific Ltd).

Mt Keith station													
Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
1989	9.5	31.0	32.5	32.5	13.5	44.0	0.0	0.0	0.0	0.0	13.2	0.0	173.7
1990	100.8	18.3	7.8	1.4	9.2	6.2	12.7	26.5	1.8	1.6	1.0	0.0	187.3
1991	0.0	0.0	14.0	8.1	0.0	33.5	22.6	0.0	5.0	0.0	0.0	8.8	92.0
1992	20.3	5.6	75.6	126.4	16.8	32.2	0.0	29.8	40.4	0.0	4.2	0.9	398.7
1993	0.0	62.0	7.8	41.0	37.2	35.0	-	-	-	-	-	-	
Mt Weld station													
1989	4.4	0.0	0.0	23.0	40.6	29.8	0.0	0.0	0.0	0.0	19.6	2.2	119.4
1990	79.6	2.4	0.0	24.0	21.6	11.8	33.4	343.7	0.3	29.4	0.2	12.1	248.5
1991	0.4	0.0	3.5	25.5	52.0	37.7	12.8	0.8	2.8	7.0	0.5	40.6	183.6
1992	13.5	56.5	64.4	102.7	47.1	29.6	3.2	99.4	46.1	13.5	3.5	1.5	481.0
1993	0.1	20.5	36.0	28.2	100.2	43.7	-	-	-	-	-	-	

1992 and 1993 due to minimal seedling establishment and unfavourable seasonal conditions. The MWS study sites were visited twice per year. All study sites (excluding MKS1 in breakaway country) were fenced to reduce the impact of sheep and kangaroos.

Plant height (H), widest point (W_1) and perpendicular (W_2) width were measured and categorised into two groups. The inverted cone shape described *E. exilifolia*, *E. latrobei latrobei* and *E. spectabilis brevis*, and canopy volume was calculated using the geometric formula ($\pi/3 r^2 h$) (Ludwig *et al.* 1975). The upper half spheroid form (Witkowski *et al.* 1991), $4/3 \pi (W_1/2) (W_2/2) (H/2)$, was used for *E. fraseri galeata*, *E. forrestii* and *E. margarethae*. Changes in mean shrub height (cm) and canopy volume (m^3) between summer 1990 and winter 1993 were calculated and tested using a one-way ANOVA. Differences between means were contrasted using Scheffe's test.

Germination and seedling establishment

Newly established seedlings were counted on each visit, tagged, labelled and the heights measured. The number of seedlings produced per fruit was individually assessed. The proportion of seedling which had germinated during the winter of 1992 and survived into winter 1993 was assessed.

Seed bank variation of *E. fraseri galeata* (MKS3)

The seed bank variation for an *E. fraseri galeata* community was investigated during December 1992. Thirty adult shrubs within the height range of 1.5–2.0 m were selected adjacent to MSK3. A further 30 sites, each situated 3 m from the selected shrubs within a bare scalded area, were chosen at random for seed-bank sampling. Since the shrub canopy of this species overhangs the main stem with a radius of approximately 0.5 m, a 1 m soil pit (depth 10 cm) immediately around the central stem was selected. Soil and litter fractions were separated, bagged, and taken to the laboratory for sieving. The soil was sieved using an automated sieve (aperture 140 mm, mesh size 2.5 mm (No.14), diameter 21.5 cm). This fraction was further sieved by hand (wooden sieve, diameter 48.5 cm, mesh size 2.0 mm) for fruit collection.

A statistical comparison of the fruit bank number between the combined soil and litter fraction in vegetated and non-vegetated sites were assessed using a t-test. An evaluation of fruit density within the two litter and soil fractions from the bare ground and under *E. fraseri galeata* shrubs were assessed using a Duncan's Multiple Comparison Test.

Results

Although germination occurred for a number of species during the winter and summer of 1991, these values were minimal and are not discussed in detail. Plant growth and seedling establishment occurred after favourable rainfall events during winter 1992 (Table 1). Mt Keith received 400 mm (twice the yearly average), a situation that has occurred only on eight occasions over the last 100 years. Mt Weld received 480 mm, the highest recorded rainfall since records began in 1900 (Table 2).

Table 3

Shrub community density, recruitment and mortality of *Eremophila* species at the Mt Keith (MKS) and Mt Weld sites (MWS); Su = summer, Au = autumn, Wi = winter, Sp = spring. Seedling survived refers to those seedling that had germinated in previous seasons and were still surviving at the time of the observation

Season		Shrub number per plot		
adults		seedlings		
		germinated	survived	dead
<i>E. exilifolia</i> (MKS1)				
Su90	73	0	-	-
Au91	73	0	0	0
Wi91	73	0	0	0
Sp91	72	1	0	0
Su91	72	0	1	0
Wi92	69	98	1	0
Su92	64	63	86	12
Wi93	64	21	80	69
<i>E. forrestii</i> (MKS2)				
Su90	32	0	-	-
Au91	32	0	0	0
Wi91	31	0	0	0
Sp91	31	0	0	0
Su91	31	0	0	0
Wi92	19	32	0	0
Su92	17	17	32	0
Wi93	17	14	49	18
<i>E. fraseri galeata</i> (MKS3)				
Su90	132	0	-	-
Au91	132	0	0	0
Wi91	131	0	0	0
Sp91	130	0	0	0
Su91	130	0	0	0
Wi92	122	148	0	0
Su92	115	237	121	27
Wi93	108	11	183	175
<i>E. latrobei latrobei</i> (MKS4)				
Su90	42	0	-	-
Au91	42	0	0	0
Wi91	42	0	0	0
Sp91	42	0	0	0
Su91	42	2	0	0
Wi92	33	108	2	0
Su92	33	145	100	8
Wi93	31	33	66	79
<i>E. spectabilis brevis</i> (MKS5)				
Su90	118	0	-	-
Au91	118	0	0	0
Wi91	118	0	0	0
Sp91	118	0	0	0
Su91	118	0	0	0
Wi92	111	756	0	0
Su92	110	34	625	131
Wi93	109	16	349	310
<i>E. forrestii</i> (MWS1)				
Su90	31	0	-	-
Wi91	31	2	0	0
Su91	31	1	2	0
Wi92	28	27	0	3
Su92	28	42	27	0
Wi93	28	3	42	27
<i>E. margarethae</i> (MWS3)				
Su90	42	0	-	-
Wi91	42	4	0	0
Su91	42	0	2	2
Wi92	38	13	0	2
Su92	38	13	13	0
Wi93	38	0	12	14

Eremophila exilifolia (MKS1). The adult plant density was 73 plants in 1991 (Table 3). Following significant rainfall (103 mm) in winter 1992, seedling recruitment was high (98 seedlings), increasing the population to 213, and this was largely maintained into winter 1993 (165 plants). Between winter and summer 1992, a period with little rain, adult plant mortality was 5. The majority of fruits produced individual seedlings during the period winter 1992-winter 1993, consisting of 87, 89 and 100% of total fruit recruitment. Twin seedlings were recorded during the winter and summer of 1992, and comprised 10% and 8% of total seedling production. All fruits with multiple seedlings (twins to quadruplets), which survived for one year, lost seedlings and had become individual seedlings by the winter of 1993.

Eremophila forrestii (MKS2). The population of 32 adult plants during 1990 at Mt Keith declined marginally to 31 plants by summer 1991 (Table 3). During the first half of 1992, the adult population was reduced to 19 plants. However, this trend was offset by favourable rains of March (76 mm) and April 1992 (126 mm). When the 32 new seedlings were examined, all the fruits were found to produce individual seedlings. New germinants were also recorded during summer 1992 (63 seedlings) and winter 1993 (14 seedlings). The total population of 31 plants in summer 1991 had risen to 80 in winter 1993.

E. fraseri galeata (MKS3). This shrub community was characterised by two age cohorts, four adult "mother" plants (average height 1.8 m) and 128 young shrubs (average height 16 cm), estimated to be 4-5 years old. The adult community appeared stable, with a gradual decline in numbers from 132 to 108 plants from summer 1990 to winter 1993 (Table 2). This decline was compensated by a marked germination event of 148 seedlings during winter 1992. These germinants were clustered around the "mother" plants and were characterised primarily by individual seedlings per fruit (103 individuals; 70% of total germinants). However, twin (24%), triplet (5%) and quadruplet germinants (1%) were also recorded. Germination was observed in summer 1992

when 237 germinants emerged. While the majority of multiple seedlings were reduced in number, primarily to individual seedlings per fruit, some fruits which initially were individual seedlings continued to produce more seedlings. For example, of the 78 single seedlings which germinated in winter 1992 and survived during the summer of 1992, five were recorded as twins while one individual fruit produced triplet seedlings. In the area containing the majority of germinants, shade, nutrients and cover from annuals, e.g. *Aristida arenaria*, *Eragrostis dielsii*, *Eriachne pulchella* and *Calandrinia* species, were abundant.

Eremophila latrobei latrobei (MKS4). The plant community of 42 plants remained stable from summer 1990 to summer 1991 (Table 3). A marked decline in adult numbers (33 plants) occurred during winter 1992 and into winter 1993 (31 plants). However, this pattern of adult mortality was compensated by recruitment of 108 and 145 germinants during winter and summer 1992. The majority of germinants comprised individual seedlings though multiple germinants were recorded, ranging from twins to quintuplet (one) fruits. In terms of total shrub density, this community peaked at 278 plants during summer 1992, but declined to 130 plants during winter 1993, a decline due primarily to seedling mortalities (44% loss).

Eremophila spectabilis brevis (MKS5). The adult population remained stable at a density of 118 plants from summer 1990 to summer 1991, declining slightly to 111 plants by winter 1993 (Table 3). Germination following favourable early winter rains during 1992 offset this decline and 756 seedlings was recorded. High survival rates (83%) of these seedlings during the summer 1992 period with the addition of a further 34 germinants, resulted in a population increase to 769 plants. However, by winter 1993 only 349 seedlings (53%) survived. The majority of fruits produced individual seedlings (98, 91 and 94% for the winter, summer 1992 and winter 1993 respectively) and the remaining germinants were twins and triplets.

Table 4

Mean shrub height and canopy volume for *Eremophila* species between summer 1990 and winter 1993 at Mt Keith and Mt Weld stations. Means between species with the same letters do not differ significantly ($p < 0.05$) by Scheffe's test. Values are mean with the standard error in parentheses.

Site	MKS1	MKS2	MKS3	MKS4	MKS5	MWS1	MWS3
Species	<i>E. exilifolia</i>	<i>E. forrestii</i>	<i>E. fraseri</i>	<i>E. latrobei</i>	<i>E. spectabilis</i>	<i>E. forrestii</i>	<i>E. margarethae</i>
subspecies			<i>galeata</i>	<i>latrobei</i>	<i>brevis</i>		
Sample size (n)	67	17	108	30	108	28	4
Mean shrub height (cm)							
Summer 1990	78.13 (5.23)	55.06 (9.40)	24.51 (3.21)	155.93 (10.29)	54.40 (1.86)	77.89 (7.13)	62.91 (2.81)
Winter 1993	85.96 (5.18)	58.70 (10.16)	31.88 (3.26)	156.50 (10.03)	58.85 (1.79)	81.57 (6.10)	69.14 (2.11)
Mean	82.04 (3.91) ^a	56.88 (1.82) ^b	28.20 (3.86) ^c	156.21 (0.28) ^d	56.47 (1.57) ^b	79.73 (1.84) ^a	66.02 (3.11) ^c
Mean shrub canopy volume (m ³)							
Summer 1990	0.44 (0.08)	1.24 (0.51)	0.36 (0.17)	0.48 (0.10)	0.07 (0.01)	1.76 (0.36)	0.46 (0.09)
Winter 1993	0.56 (0.09)	1.42 (0.54)	0.45 (0.21)	0.61 (0.10)	0.11 (0.01)	1.94 (0.38)	0.60 (0.09)
Mean	0.50 (0.06) ^a	1.33 (0.09) ^b	0.40 (0.04) ^a	0.54 (0.06) ^{ac}	0.09 (0.02) ^d	1.85 (0.09) ^c	0.53 (0.07) ^{ac}

Eremophila forrestii (MWS1). A similar trend was observed at Mt Weld station with the most significant germination event occurring after the winter rain of 1992. Following this period, a total of 27, 69 and 45 seedlings were recorded to winter 1993 (Table 3). The majority of new germinants were noted to be single seedlings.

Eremophila margarethae (MWS3). The adult plant density remained relatively stable (42 to 38 plants) from winter 1991 to 1993 (Table 3). Germination peaked in the winter and summer 1992, but was followed by a seedling mortality of 54% between winter 1992 and winter 1993.

Mean shrub height and canopy volume

The smallest mean shrub height was 28.20 ± 3.68 cm ($n=108$) for *E. fraseri galeata* and the largest shrub height was recorded for *E. latrobei latrobei* with 156.2 ± 0.3 cm ($n=30$; Table 4). In terms of canopy volume, *E. spectabilis brevis* and *E. forrestii* (MWS3; MKS2) had the lowest and highest canopy volume, 0.09 and 1.85 (1.33) m³ respectively. The remaining species were closely related with a range of 0.40 - 0.54 m³ (Table 4).

Germination and seedling establishment

The survival rates of all single seedlings which germinated during the winter period of 1992 was observed for 1 year (Table 5). One year after seedling establishment, 60, 69 and 30% respectively of the seedlings of *E. forrestii* (MWS1; MKS2) and *E. margarethae* (MWS3) survived. All the other species followed a constant mortality rate. The greatest proportion of mortalities was related to the species which produced the highest number of germinants; *E. exilifolia*, *E. fraseri galeata*, *E. latrobei latrobei* and *E. spectabilis brevis*.

Seed bank variation for an *E. fraseri galeata* community

The number of fruits in bare ground (2.2 ± 0.4) and under an *E. fraseri galeata* canopy layer (56.0 ± 16.4) was significantly different ($p<0.01$). There was also a significant difference ($p<0.05$) in fruit numbers under the plant within the soil (42.9 ± 14.3) and litter zones (13.1 ± 3.4) compared to the non-vegetated soil (1.3 ± 0.3) and litter zone (0.9 ± 0.2). If the adult population density of 4 "mother" plants is extrapolated to 81 adults ha⁻¹, with each plant possessing a mean of 56 fruits per plant, the estimated total is 4536 fruits ha⁻¹. Assuming the remaining area consists of either bare ground or *E. fraseri galeata* community other than "mother" plants, the estimated fruit count is 21822. Since each fruit may contain up to 8 seeds, the maximum potential is 210864 seeds ha⁻¹. The

mean litter weight under the canopy was estimated as 5328 kg ha⁻¹, in contrast to 2693 kg ha⁻¹ for the bare areas.

Discussion

Eremophila species are well adapted to arid conditions, some capable of surviving without any rainfall for approximately 2 years (Elliot & Jones 1984). Adult shrub mortalities were recorded at all sites in the seasons 1990-1991, probably due to lack of rain. Favourable rainfall events at both sites during autumn and winter of 1992 resulted in significant levels of seedling recruitment for all species. The density of germinants at Mt Weld was markedly lower than at Mt Keith. This may be due to the competitive effect of *Atriplex* and *Maireana* species which dominated as an understorey species at the former site. At Mt Keith, with the exception of scattered communities of *Eragrostis erapoda* and *Triodia basedowii*, the understorey consists primarily of *Eremophila* species.

Following the high rainfall of winter 1992, the *E. spectabilis brevis* (MKS5) community (15420 germinants ha⁻¹) increased to a shrub population of 17684 ha⁻¹. All fruits which produced seedlings appeared to be highly weathered, indicating that they were several years old. This, combined with the rain which leaches out germination inhibitors in the fruit wall (Richmond 1993; Richmond & Ghisalberti 1994b), might explain the high recruitment rate. *E. spectabilis brevis* appears to be a highly competitive and aggressive species when favourable seasonal conditions occur (Richmond 1993). The fruits can contain up to 12 seeds compared to a maximum of eight for the other species under investigation. This may be a contributing factor to the higher germination rate. Its seedling recruitment pattern resembles that of the Queensland species *E. gilesii*, to which it is taxonomically closely related (Section Eremaeae; Chinnock pers. comm.). Many seedlings appeared from one fruit, illustrating the highly competitive nature of this species.

While most germination involved fruits possessing single seedlings, some fruits produced multiple seedlings, with quintuplets being recorded for fruits of *E. fraseri galeata* during the summer of 1992. Burrows (1971) also observed multiple seedlings (11.8% twin and 2.5% triplets) produced from fruits of *E. gilesii* after a 40 mm rainfall event. An interesting observation in the present study is that, when climatic variables are favourable, the fruits may continue to produce multiple germinants several months after initial germination.

Seedlings of *E. forrestii* (MKS2 and MWS1), *E. latrobei latrobei* (MKS4) and *E. margarethae* (MWS3) appear resilient to desiccation, since 100, 93 and 100% survived 6 months after germination. Field observations suggested that their survival may be due to a characteristic thickening of the hypocotyl and rapid root establishment. These hypocotyls were hirsute, thus possibly reflecting damaging light and reducing evapo-transpiration (Clifford 1987). *Eremophila forrestii* and *E. latrobei latrobei* appeared to have the fastest growth rates in terms of height gained over 1 year, with a mean of 8.3 cm, compared to 5.9 cm for the remaining species.

Whilst germination was observed for all species within the study sites, seedling survival was

Table 5

Proportion of seedlings surviving over 12 months (Wi = winter, Su = summer)

Species	Site	Wi92	Su92	Wi93
<i>E. exilifolia</i>	MKS1	1.00	0.75	0.42
<i>E. forrestii</i>	MKS2	1.00	1.00	0.69
<i>E. fraserii galeata</i>	MKS3	1.00	0.76	0.49
<i>E. latrobei latrobei</i>	MKS4	1.00	0.93	0.72
<i>E. spectabilis brevis</i>	MKS5	1.00	0.83	0.46
<i>E. forrestii</i>	MWS1	1.00	1.00	0.60
<i>E. margarethae</i>	MWS3	1.00	1.00	0.30

characterised by an aggregation around old plant remains and under canopies of existing shrubs and small trees. Within the *E. fraseri galeata* community, germinants aggregated within the canopy drip line of adult plants as noted by Hacker (1984). Increased accumulation of nutrients, water availability and soil depth beneath adult plants may contribute towards the establishment and maintenance of *E. forrestii* within the arid shrublands (Hacker 1979, 1984).

A study of the seed bank variation within the soil and litter layer of an *E. fraseri galeata* community revealed a mean concentration of 56 fruits m⁻² under each shrub compared to 2 fruits m⁻² in bare ground. This highlights the point that the litter and detritus layers may play a role in maintaining favourable edaphic factors and microclimate, thereby promoting seedling germination and survival when better environmental conditions occur (Hacker 1984). The total fruit count was 26402 fruits ha⁻¹ and is an important topsoil seed bank for this community. The fruit bank for *E. gilesii* is far greater, with 4285000 ha⁻¹ being calculated by Burrows (1971) for a plant community comprising 60000 adults ha⁻¹. It is interesting to note that *E. gilesii* is a prolific seeder with a life span of approximately 10 years (Burrows 1974), whereas *E. fraserii* has a life span of 100 years (Chinnock 1974). For *E. sturtii* and *E. mitchellii*, 170000 fruits ha⁻¹ have been recorded (Hodgkinson *et al.* 1980).

Germination and growth of *Eremophila* species occur on relatively impoverished soils when favourable conditions occur. This has been illustrated by the large increase in population of *E. spectabilis brevis* after high rainfall, and is indicative of the ability of this genus to regenerate at high levels. A species' ability to survive both in time and space is associated and enhanced by the germination characteristics, particular if multiple seedlings emerge from one fruit.

Acknowledgements: J Fox, B Tan (Curtin University of Technology) and R Chinnock (Adelaide Botanic Gardens and State Herbarium) are thanked for ecological discussions. The project was supported by the Minerals and Energy Research Institute of Western Australia (Project M156) and the following organisations; Australian Consolidated Minerals-Mt Keith operation (Western Mining Corporation); Central Kalgoorlie Gold Mines, Coolgardie Gold; Goldfan; Kaltails Mining Services; Placer Pacific; and Western Mining Corporation at Kambalda. Special thanks to C Woolard (WMC), P Davidson and D Ferguson for logistical support at Mt Keith. A Leeds (Mt Keith) and L Polomer (Mt Weld) gave permission for fieldwork to be carried out on the properties. The dedication of the many field assistants, G Verrall, L-A Stewart, L Broadhurst, M Pennacchio, P Middleton, D Fletcher, J Brand, T Grubba and P Varris, is acknowledged.

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Plant breeding for stable agriculture: Presidential Address 1994

W A Cowling

Agriculture Western Australia, 3 Baron-Hay Court, South Perth WA 6151

Manuscript received October 1996

Introduction

Plant breeding contributes to stable agriculture by improving adaptation of plants to the agricultural environment. There are many successes and failures in modern plant breeding - the key is to learn from the mistakes and build on the successes.

It is my privilege to talk on the subject of plant breeding and its role in developing stable agricultural systems. Plant breeding has fascinated the human race and has been pivotal to its development since the early hunter-gatherers selected the first domesticated plants about 10,000 years ago (Duvick 1996). Plant breeding may also provide a key to survival of the human species. There is a widely held view that agriculture is intrinsically unstable and that plant breeding can do little to help, especially with regard to disease resistance. My talk challenges this view and provides a more optimistic outlook for agriculture. In order to be "stable", agricultural systems must be dynamic, have minimal impact on the surrounding environment, and be well buffered against attacks of pests and diseases. I believe that plant breeding will underpin future progress towards stable agriculture by developing crops that are better adapted to their environment and have more durable disease resistance. However, some changes in the approach to plant breeding may be needed.

Plant breeding is a very public activity, and the result of a plant breeder's labour - a new crop variety - is subject to more critical review by the public than results of most other biological science professions. There have been some spectacular failures in modern plant breeding, most notably the failure of disease resistance genes. This has over-shadowed the steady progress in yield and quality that continues to be made in modern plant breeding. I define "modern plant breeding" as the era of Mendelian genetics from the early 1900's to the present day. Resistance to rust in wheat was one of the first economically important characters proven to be under the control of a single gene. Such genes had major qualitative effects that followed Mendel's Laws. There was much excitement with the discovery of the gene as the basic unit of inheritance, and zealous Mendelian crusaders used disease resistance genes to verify the importance of their theory, and to criticise the proponents of Darwinian "gradualism" (Robinson 1996).

It was soon learned that some characters were not controlled by single genes, and that not all genetic effects were qualitative. Some characters displayed quantitative rather than discrete variation. Bitter arguments erupted between the new Mendelian geneticists and followers of Darwinian "gradualism", and these arguments were not resolved until the development of the science of popula-

tion genetics. Population genetics theory explained the movement of genes in populations, and also explained the genetic control of quantitative characters. Such characters did not form discrete groups in Mendelian tests, and were influenced by the environment. Biometricians developed the statistical theory that formed the basis of population breeding methods in animals and cross-fertilising plants such as lucerne. However, breeders of self-fertilising crops remained largely locked into pedigree breeding procedures developed by the early Mendelian geneticists 90 years ago - especially with respect to disease resistance (Robinson 1996).

In many crops, single "Mendelian" genes for disease resistance have often "broken down" due to the development of new races of the pathogen. The situation with wheat stem rust and potato late blight is documented and discussed by Vanderplank (1963). This has happened so many times and in so many crops in the past 90 years that most farmers and scientists alike have come to believe that all disease resistance is temporary - that eventually all disease resistance breaks down. There is no doubt that Mendelian disease resistance genes have been of great economic value in some crops, although the hidden costs of such breeding may be high. Nevertheless, the failure of some types of disease resistance genes have prompted many authors such as Vanderplank (1968) and Robinson (1987) to promote alternative approaches to breeding for durable resistance.

Plant breeders are reluctant to change from pedigree breeding methods because they continue to make breeding progress with these methods (Kannenberg & Falk 1995). In pedigree breeding, selfing occurs for several generations to allow selection on near-homozygous and uniform lines. The tendency is to restrict parents to a few "tried and proven" varieties, and cycles of crossing and selection are long (10 to 15 year cycles). This has led to narrowing of the genetic base in modern cultivars, which is a concern for many breeders (Shands & Weisner 1991, 1992). In the common bean there has been no yield progress for several decades due to the narrow germplasm base (Silbernagel & Hannan 1992; McClean *et al.* 1993).

Population breeding, on the other hand, draws on a broad genetic base and employs rapid cycles of crossing and selection (1 to 4 year cycles). Parents may be heterozygous early generation lines rather than "tried and proven" varieties. The introduction of new germplasm raises the genetic ceiling on yield improvement, improves ecological adaptation, and decreases vulnerability to pests and diseases (Kannenberg & Falk 1995). Population improvement is a powerful procedure for breeding programs to exploit genetic variability (Frey 1983). Population breeding methods have been shown to improve polygenic and durable resistance, and to secure

long-term improvements in yield and adaptation (Carver & Bruns 1993; Cassler & Pederson 1996; Robinson 1987). Such methods should contribute to the long term stability of agriculture.

Stable agriculture - past and present

Instability in agricultural systems has caused major social and environmental problems since the beginning of civilisation. Despite this, some stable agricultural systems are evident and some have involved lupins.

Is stable agriculture possible? To answer this question, it is important to examine the factors that have rendered agriculture unstable. These include genetic vulnerability in crop plants (usually referring to vulnerability to new diseases or changes in strains of pathogens), cultivation techniques or grazing pressures that cause soil erosion by wind or water, rising water tables and salinity caused by land clearing or irrigation, continuous cropping leading to soil acidity and depletion of soil fertility and structure, and more recently, chemical contamination of ground water and produce and development of pesticide resistance.

The genetic vulnerability of crop plants to disease was highlighted as the level of international trade increased in the 18th and 19th century. Potatoes provide an interesting example of extreme susceptibility in a crop plant that is exposed to a new pathogen for the first time. Potatoes were introduced into Europe from South America by the Spanish in the 16th century. Two centuries of selection by European horticulturalists altered the potato from a tropical plant to a long-day plant that matured before the frosts of winter (Robinson 1996). Potatoes grew particularly well in Ireland where the climate was moist and there was little frost. Social changes at the time of the industrial revolution demanded plentiful supply of cheap food, and potatoes became cheaper than bread. In Ireland, where it was difficult to grow cereals, the population flourished as the potato flourished. However, the potato in South America (where the European potato originated) had never encountered the late blight fungus, and when the late blight fungus arrived in Europe from Mexico in the 1840's, it rapidly spread through vast regions of uniformly susceptible potato crops - with devastating consequences (Large 1940). Ireland's social structure and economy collapsed as millions died or emigrated to the USA or Australia.

Instability of agriculture in WA is very evident as a result of rising water tables and salinity following land clearing. This is a major threat to long-term sustainability of agriculture. Increasing water use from agricultural lands and nature reserves is a major priority for reducing the problems in WA (George *et al.* 1996). Alley farming and agro-forestry will help to lower salt-laden water tables and provide useful shelter for stock and wind breaks for crops (Lefroy & Scott 1994). The cost of revegetation will be large, and must be accompanied by the development of profitable and sustainable cropping systems on the best soils.

Some agricultural systems have remained relatively stable for many years - take for example cork oak plantations in Portugal (Pinto 1994). The cork oak soils in southern Portugal are very poor - not unlike soils in the

south-west of WA. Cork is harvested from the trees every nine years. During this nine year cycle, up to two crops of semi-bitter yellow lupins (*Lupinus luteus*) with shattering pods are planted and allowed to self-seed for a second year. Sheep graze the lupin seed and stubble at the end of each year. Cultivation occurs only to plant the lupin and to control flammable vegetation. This agro-ecosystem has survived without chemicals or fertilisers and has proven to be a very sustainable and low-input agricultural system (Pinto 1994).

Plant breeding and stable agriculture

Despite the repeated break-downs in disease resistance, modern plant breeding has resulted in steady improvements in yield and quality of many crops. However, genetic diversity in modern crops is low and rates of improvement may fall. Population breeding methods may improve the yield and stability of crops through more diversified gene pools and durable polygenic disease resistance.

Plant breeding should underpin progress towards stable agriculture by providing farmers with well adapted and high yielding crop varieties. But how well has plant breeding achieved stable improvements in the past, and how should breeding practices be altered to maintain or accelerate these improvements in the future? Examples will be given to show that improvements in grain yield have been occurring steadily in most crops since modern plant breeding began about 90 years ago. Biotechnology will be one more addition to the tool kit of plant breeders to help them to continue this progress into the future (Duvick 1996).

In the process of achieving these improvements, plant breeders have restricted their genetic diversity to a narrow range of elite parents. There is a growing concern that genetic diversity is dangerously restricted in modern crop cultivars (Shands & Weisner 1991, 1992). Crops that demonstrate continued improvements with modern plant breeding have achieved this progress in the early cycles of selection. In most crops only 5 to 8 "effective" cycles of selection have occurred since the early 1900's. There is a strong incentive to restrict the crossing parents to tried and proven varieties in pedigree breeding and pure line methods. It is very difficult to find improvements in single crosses outside of the main adapted cultivars. It is possible that many crops have not yet reached a yield plateau because of these slow cycles of selection. The yield plateau in common bean (Silbernagel & Hannan 1992; McClean *et al.* 1993) provides a timely warning - there is an urgent need to introduce additional genetic variability into breeding systems (Kannenberg & Falk 1995).

Yield improvements in modern crop cultivars are often dependent on major genes for disease and pest resistance, and the extensive use of pesticides. Pedigree breeding attempts to maintain disease resistance through a procedure known as backcrossing, whereby new disease resistance genes are transferred from a "good source" into the elite cultivar following the "break down" of previous resistance genes (Robinson 1996).

In order to contribute to stable agriculture, plant breeding should improve yield and quality in target environments in tandem with durable disease resistance.

Most economically-important traits, including yield, quality and disease resistance, may be considered as polygenic characters that are subject to the laws of population genetics (rather than Mendelian genetics). In many cases, the rate of yield improvement may be increased and genetic vulnerability decreased by the application of population breeding methods. Recurrent selection is a common population breeding method that increases the frequency of favourable genes in a population (Frey 1983). The rate of improvement depends on genetic diversity, selection pressure and the duration of selection cycles. Population breeding methods should enhance the development of favourable combinations of genes that are likely to contribute to the long-term stability of agriculture.

Plant breeding progress

Breeding progress has been apparent in the major crops in most countries over the past 90 years. Examples include wheat, barley, soybean, cotton, sorghum and corn.

Grain yield of soft red winter wheat varieties in Ohio increased by 2259 kg ha⁻¹ from 1910 to 1991 (1.3% per year from 1947-1987), based on historical variety trials conducted at high rates of fertilisation but without fungicides (Fig 1). Higher yields were associated with earlier flowering, reduced height, and greater resistance to lodging in modern varieties (Berzonsky & Lafever 1993).

Yield of barley varieties in Eastern Canada increased steadily by 1.0% per year from 1956 to 1988, with no signs of a yield plateau. Harvest index increased from 0.44 to 0.51, and biomass also increased. Modern cultivars are heavier, have stronger stems and tend to be shorter, with greater lodging resistance (Bulman *et al.* 1993). Similar genetic improvements are noted in yield of corn (Tollenaar *et al.* 1994), soybean, sorghum, cotton and wheat in the USA (Fehr 1984), and in yield and quality of wheat in South Africa (van Lill & Purchase 1995).

It is important to remember that varieties bred in one country are not necessarily adapted in another. Estimations of breeding progress are affected by the locations of historic variety trials. Genotype $\times$ environment interac-

tions affect estimates of breeding progress, or to use an analogy, there are "horses for courses" - each variety has its preferred region of adaptation. The "horses for courses" analogy applies at the international level as well as at the regional level within WA. Genetic improvement must be measured in relevant environments.

Breeding progress in WA

Plant breeding in WA has an impressive record of crop improvement in recent years. Breeding progress is usually measured in historic variety trials, and the results are highly dependent on how, where and what measurements are made. Improvements in lupins, barley and wheat in WA demonstrate these points.

The techniques chosen to estimate breeding progress can have a major influence on the outcome of the experiments. In 1991 and 1992, I conducted a series of historic variety trials in the cropping region of southwest WA using an historical set of narrow-leaved lupin (*L. angustifolius*) varieties released earlier by Dr John Gladstones. Each variety was sown at a wide range of seeding rates. Merrit, released in 1991, was significantly higher yielding than Unicrop, released in 1973. At a target density of 70 plants m⁻², the yield of Merrit was 43% higher yielding than Unicrop, a yield improvement of 2.4% per year from 1973 to 1991 (Cowling & Speijers 1994). At a seeding rate of 120 kg ha⁻¹, the estimate of breeding progress was 1.9% per year between Unicrop and Merrit. However, at low seeding rates of 30-40 kg ha⁻¹, there was no difference in yield between the two varieties, and no apparent progress in yield improvement (Fig 2).

It follows that estimates of breeding progress depend on the seeding rates at which varieties are tested. As with lupins in WA, modern varieties of corn perform better than older varieties at high densities (Tollenaar *et al.* 1994). It makes good economic sense for a farmer to sow Merrit lupins at higher seeding rates than Unicrop.

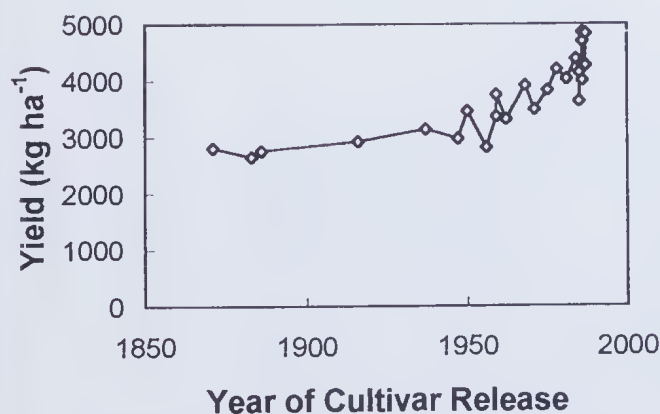


Figure 1. Grain yield (kg ha⁻¹) of soft red winter wheat varieties in Ohio based on historical variety trials (Source: Berzonsky & Lafever 1993).

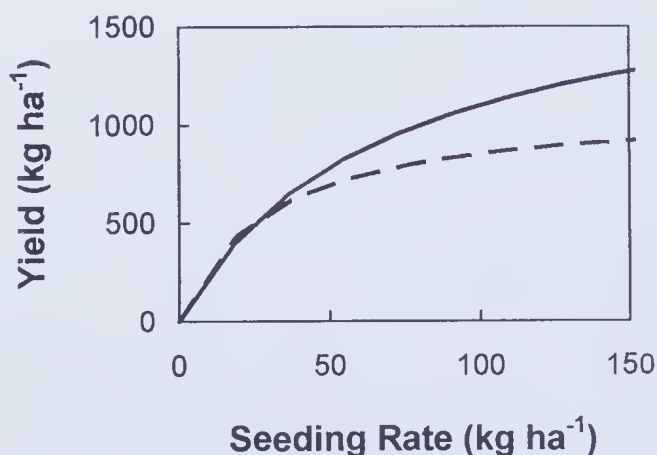


Figure 2. Influence of seeding rate (kg ha⁻¹) on yield (kg ha⁻¹) of narrow-leaved lupin cultivars Merrit (solid line; released in 1991) and Unicrop (broken line; released in 1973) in historic variety trials in Western Australia. (Source: Cowling & Speijers 1994).

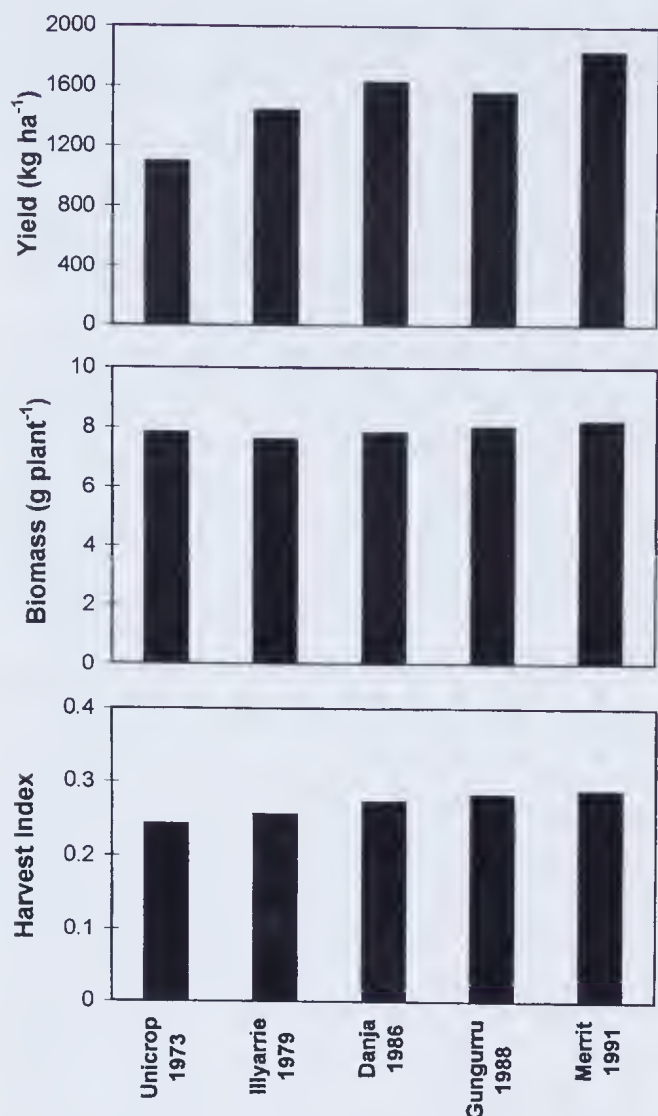


Figure 3. Results of historic variety trials in Western Australia of narrow-leaved lupin cultivars Unicrop (released 1973), Illyarrie (1979), Danja (1986), Gungurru (1988) and Merrit (1991): top Relative yield (kg ha⁻¹) at predicted maximum yield; centre Biomass (g plant⁻¹ dry weight) at harvest; and bottom Harvest Index. (Sources: Cowling & Speijers 1994, and Tapscott *et al.* 1994).

Conversely, any factors that decrease the plant density of Merrit, such as poor germination or root rot disease, will decrease its relative yield advantage.

While there has been a progressive improvement in yield of lupin varieties from Unicrop to Merrit (Fig 3 top), total plant weight or biomass of the historical cultivars has not changed (Fig 3 centre) over this 18 year period (Tapscott *et al.* 1994). Total weight includes seed, leaves and stems at harvest. Harvest index, or the proportion of the mature plant dry weight in seed, has increased steadily from Unicrop to Merrit (Fig 3 bottom) (Tapscott *et al.* 1994). Merrit is more efficient at converting vegetative mass to seed than Unicrop. However, harvest index is still low in comparison with other grain legumes, and harvest index of lupins in WA may be higher in future higher-yielding varieties.

Estimations of breeding progress are also affected by locations of variety trials. In this example, some barley

varieties perform better in low rainfall regions, others perform better in high rainfall regions of WA (R F Gilmour, *pers. comm.*).

In the high rainfall region, progress in barley breeding in WA has been very impressive - yield has improved by 2.5% per year from Dampier (released 1966) to Onslow (released 1990). Onslow yields more than twice that of Prior, released in 1900 (Fig 4 top). In the low rainfall region, yield improvement has not been as rapid, but is still very reasonable (Fig 4 bottom), increasing 1.5% per year from Dampier (1966) to O'Connor (1984). Onslow is not adapted to low rainfall regions, and yields less than Prior in low rainfall! It would be quite misleading to measure breeding progress in barley based on the average yield of these varieties across rainfall regions. Breeding progress in barley is occurring in different gene pools in the high rainfall than in the low rainfall.

When estimating breeding progress, it is also important to define what is being measured. The wheat breeding program in Agriculture WA is the first in the world to breed a variety specifically for the Japanese noodle market. The variety Cadoux was released in 1992. Cadoux is higher yielding than its predecessor, and gives WA a competitive edge in the Japanese noodle market over its rivals in Canada and the USA. Growers receive a price bonus for Cadoux wheat. This is equivalent to 10-

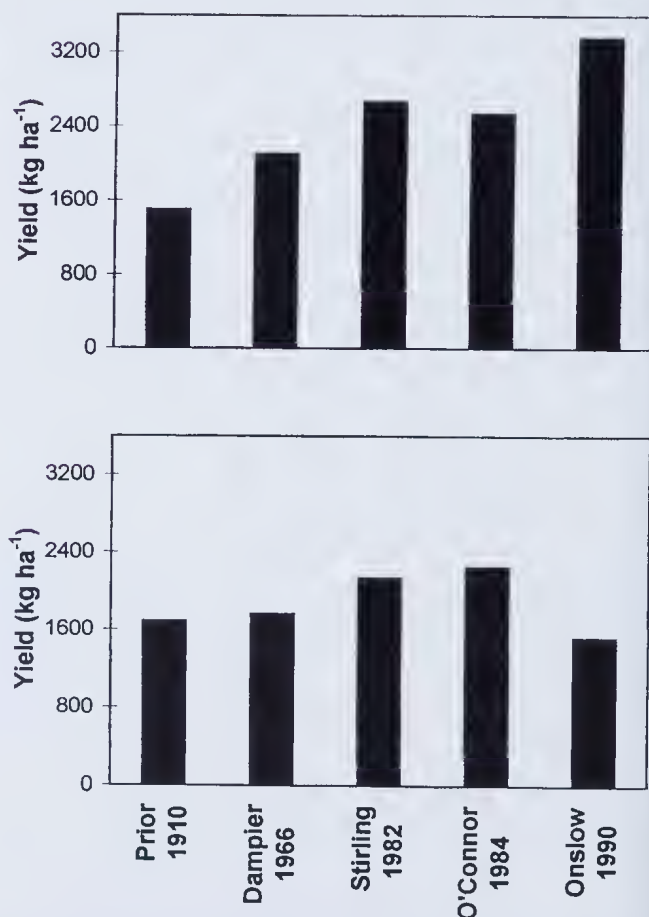


Figure 4. Yield (kg ha⁻¹) of barley varieties in historic variety trials in high rainfall (top) and low rainfall (bottom) regions of Western Australia (Source: R F Gilmour, *pers. comm.*).

20% yield improvement in normal Australian Standard White varieties. The market potential was recognised by the breeders and cereal chemists at least 10 years in advance. Selection techniques for Japanese noodle qualities had to be developed and working effectively long before the new wheat was released (G Crosbie, *pers. comm.*). The Japanese noodle wheat has lifted the profitability of cropping and provided cash for stability projects on the farm.

Lupins and stable agriculture in WA

Lupins have rapidly expanded in area and production in WA over the past two decades. Lupins filled the need for a productive legume in rotations with cereal crops on light sandy soils. Improvements in crop rotations due to lupins will improve the profitability and stability of agriculture. Improvements in farm profits may allow increased expenditure on land and soil conservation measures.

Narrow-leaved lupin production increased exponentially during the 1980's in WA to more than one million tonnes per annum by the early 1990's. Average lupin yield per hectare in WA improved by about 20% during the 1980's (Fig 5). This was partly the result of better lupin agronomy and partly due to better lupin varieties. Lupins are now the second largest crop in WA based on area of production (Australian Bureau of Statistics 1996). Farmers have responded quickly to incorporate this legume into their farming systems. In doing so, they have improved their economic viability and the long-term stability of agriculture.

Lupins provide a direct benefit for the stability of agriculture in WA, mostly through improvements in crop rotations with cereals. Wheat following lupins is higher yielding, has lower disease levels, fewer weeds and higher grain protein than wheat following another cereal or poor pasture (Nelson 1994). Consequently, the crop rotation is more profitable and more stable in the long term when lupins are included in the system.

Lupins also improve soil structure and fertility, are a cash crop in their own right, and the stubbles and seed provide valuable on-farm feed for livestock over sum-

mer. Lupins lift whole-farm profitability and help to provide farmers with the extra cash needed to help them modify their farms for long-term stability.

The total biomass production of a lupin:wheat rotation exceeds that of continuous cereal cropping or cereal crop following poor grassy pasture; as a result, the lupin:wheat rotation should use more of the available soil moisture and there should be less recharge to the water table. The introduction of lupins into the rotation should reduce potential problems from rising water tables and salinity (George *et al.* 1996).

Recently, yellow lupins (*L. luteus*) have been found to be very well adapted to the very acidic soils of the eastern wheatbelt of WA (Sweetingham *et al.* 1994). Yellow lupins are resistant to brown spot (Yang *et al.* 1996) and *Pleiochaeta* root rot (Sweetingham *et al.* 1994) and yield more than narrow-leaved lupins on these very acidic soils. This is the first legume crop for very acid soils, and as with the narrow-leaved lupin, yellow lupins will increase productivity of crop rotations on these soils.

Lupins, as with any legume or nitrogen fertiliser, contribute to soil acidity. This is an increasing problem on WA soils, but fortunately there is a remedy - the application of lime to the soil. The added cost of lime should be funded by the increased profitability of lupin:wheat rotations on acid soils.

Lupins and new approaches to plant breeding

Lupins are a new crop for modern agriculture and are in an ideal position to test some new approaches to plant breeding.

Lupinus is a large genus in the Leguminosae with a great diversity of forms in the Americas, the Mediterranean basin and northern Africa. Perennial lupins are found above the snow-line in Alaska and along the California coast, annual types on the fringe of the Mediterranean sea and in the highlands of equatorial Africa, and simple-leaved types on the coastal plains of Paraguay, Argentina and in southern Florida (Allen & Allen 1981; Monteiro & Gibbs 1986; Planchuelo 1994; Gladstones 1974).

Lupins provide an interesting example of the parallel domestication of plants by two geographically and culturally isolated human civilisations. Lupins were developed independently as a food crop by Greek/Roman civilisations in the Mediterranean region and by native American civilisations in the high Andes mountains of South America (Hondelmann 1984). There are frequent references to lupin cultivation in early Greek and Roman literature (Hondelmann 1984). Lupini beans (*L. albus*) are consumed to the present day after debittering by traditional methods in Italy, Greece, Spain, Portugal, and in the Arabic cultures of the eastern and southern Mediterranean and northern Africa. Cultivated types of the Andean lupin (*L. mutabilis*, known as "tarwi") were selected independently by Indian civilisations in South America. One of the early Spanish conquerors noted the similarity between the lupin eaten by the Incas and those eaten in Spain (Hondelmann 1984), and it is certain that the technology to debitter lupins was developed by both cultures independently of one another.

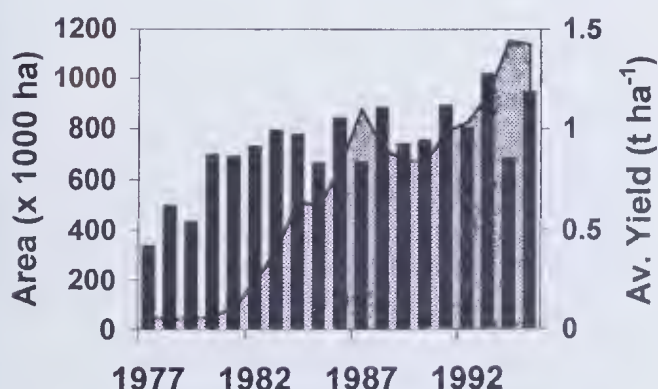


Figure 5. Average yield (solid bars; tonne ha⁻¹) and area of production (stippled area; x 1000 ha) of narrow-leaved lupin in Western Australia from 1977 to 1995 (growing seasons). Source: Australian Bureau of Statistics (1996) and earlier publications of the same series.

As a modern crop plant, lupins have a relatively short history. Researchers in Germany in the 1920's and 1930's were convinced that low alkaloid (sweet) forms of lupins could be found. They proceeded to select sweet forms of *L. angustifolius*, *L. albus* and *L. luteus* and were able to fully domesticate the latter two species. Sweet narrow-leaved lupins were not fully domesticated (with sweet and soft seeds and non-shattering pods) until the 1960's by Dr John Gladstones in WA (Gladstones 1982). The history of narrow-leaved lupin production in WA since the 1960's is a story of successful collaboration among lupin breeders, researchers, advisers, marketers and growers in WA (Nelson 1994).

There are few other breeding programs for *L. angustifolius* in the world, and most of those are based on varieties released in WA, so the domesticated gene pool is relatively small. All improvements in narrow-leaved lupins of relevance to southern Australia for the near future will depend on breeding material developed in WA (Cowling 1994).

Wild lupins are an important source of new genetic variability, and a significant proportion of the lupin breeding effort in WA is allocated to conserving and evaluating the genetic resource in the "International Lupin Collection" at Agriculture WA in South Perth (Cowling 1994). It is necessary to cross advanced breeding lines with wild plants to expand the domesticated gene pool. Crosses with wild narrow-leaved lupins from Spain, Morocco, Portugal, Israel, Italy, and Greece have formed the backbone of genetic improvements in lupins in WA and such crosses will continue to be important for some time (Gladstones 1994).

It takes several years to reselect fully domesticated progeny from crosses with wild lupins, and these "first-cross" lines may not be suitable for release due to flaws in yield, quality or agronomic characteristics. Nevertheless, they may have particular features (such as improvements in disease resistance) that may contribute to crop improvement. I have used recurrent selection to simultaneously improve disease resistance, yield and quality in such breeding material (Cowling 1994). In 1984 when I began breeding for resistance to brown spot (caused by the fungus *Pleiochaeta setosa*) in narrow-leaved lupins, there was no known "strong source" of resistance. Recurrent selection seemed the best choice of methods for this crop and this disease (see below; "Brown Spot Resistance in Lupins: a Case History of Recurrent Selection").

Recurrent selection is a form of population breeding that is the accepted standard method in cross-pollinating forage plants (Casler & Pederson 1996), but has yet to be fully exploited in self-pollinating plants. Durable disease and pest resistance should result from the application of population breeding methods to resistance (Robinson 1987, 1996). The lupin recurrent selection program in WA is one of few applied breeding programs of self-pollinating plants to use population breeding methods.

Population breeding methods

Population breeding methods, although not new, offer long-term solutions to some serious problems with modern plant breeding.

I discussed earlier the seriousness of the problems of

narrow gene pools, slow selection cycles and the unreliability of Mendelian genes for resistance in modern plant breeding. To overcome some of these problems, it is necessary to use population breeding methods. Such methods should improve long-term progress in plant breeding by (i) increasing genetic variance (diversifying the gene pool in order to increase the potential for long-term genetic gain), and (ii) accelerating cycles of selection (decreasing the time between crossing of parents and crossing of progeny). Success depends on high selection pressure which results from accurate and reliable yield measurements, uniform disease pressure, and relevant quality measurements.

Population breeding methods are designed to improve traits under polygenic control, such as yield, quality and disease resistance. Genes are mixed and re-arranged to form so-called "adapted gene complexes", and the frequency of favourable alleles in the population is increased by selection (Frey 1983). Transgressive segregation is said to have occurred when, after some cycles of crossing and selection, many lines in the final generation are higher yielding or more disease resistant than the original parents.

In recurrent selection, recurring cycles of crossing and selection allow favourable genes or gene combinations to be accumulated in the population. Recurrent selection has been used extensively (Frey 1983) in cross-pollinating crops (such as maize) and pasture plants (for example sweetclover and alfalfa). More recently, it has been applied to several self-pollinating crops such as wheat, oats, barley, soybean, sorghum, bean, tobacco, and cotton (Kervella *et al.* 1991; Goldringer & Brabant 1993). In most references in these two review articles, recurrent selection was used to improve polygenically-controlled traits such as yield, seed size, protein, and oil. There are relatively few references in the literature to improvements in disease resistance by recurrent selection, mostly because the research required for publication has not been done.

Recurrent selection in self-pollinating plants begins with a partial diallel cross among the selected parent lines, and selection normally takes place on F_2 -derived lines. The best progeny are selected by the F_2 , F_3 or F_4 for inter-crossing to begin the next cycle. If the parents themselves are F_2 -derived and quite heterogeneous, it is possible to begin selecting in the F_1 (called S_0 in breeding of cross-pollinating plants). The population may be kept "closed", that is, without introducing new genetic lines to the population after the initial diallel cross, or new lines may be added to crossing in the following cycles.

Carver & Bruns (1993) in their review found that recurrent selection in self-pollinating crops has resulted in yield improvements of 3-4% per year, and quality improvements of 5.3% per year. This compares very favourably with the breeding progress for yield in traditional breeding programs around the world referred to earlier (1-2% per year).

Pedigree plant breeding may be regarded as a form of recurrent selection, but the long-term genetic gain is limited by the slow cycles, the high number of selfing generations before intercrossing, and the narrow genetic base (Kervella *et al.* 1991). The chances of improving polygenic resistance are very low using traditional pedigree breeding in self-pollinating crops.

Breeding for polygenic disease resistance by recurrent selection

Recurrent selection has been shown to increase disease resistance (presumed to be polygenic) by transgressive segregation. Polygenic resistance developed by these techniques is durable. Horizontal and vertical resistance are descriptive terms to describe (i) polygenic resistance that is normally durable (horizontal) and (ii) major gene resistance that belongs to the "gene-for-gene" system of plant disease resistance (vertical).

In 1954, a small but significant article appeared in the American Potato Journal. It was one of the first reports of the deliberate use of population breeding methods for disease resistance, carried out by John Niederhauser and coworkers in Mexico against late blight on potatoes. Niederhauser *et al.* (1954) saw that major gene resistance to late blight was of little use in Mexico, and proceeded to select partial resistance by population breeding methods - deliberately eliminating simple major gene resistance. The partially resistant varieties remained greener in field trials than plants with "broken down" major gene resistance, which were completely dead. In addition, the partial resistance developed by population breeding was not specific to one race of the pathogen: "in the field [these varieties] show a degree of resistance that is exhibited equally toward all races of the pathogen" (Niederhauser *et al.* 1954). Niederhauser produced several cultivars with high levels of partial resistance, accumulated by population breeding methods. His cultivar "Atzimba" is the standard against which other cultivars are measured in Mexico (Robinson 1987).

A similar approach was used by Robinson in Kenya in the 1950's and 1960's against late blight and bacterial wilt of potato, and Robinson's potato varieties remain resistant and are grown on a wide scale in Kenya to this day without the need for expensive seed potato schemes (Robinson 1987, 1996).

Several studies have demonstrated improvements in disease resistance beyond that seen in the parents, achieved by transgressive segregation. Transgressive segregation was shown for resistance to yellow rust in wheat (Krupinsky & Sharp 1979; Wallwork & Johnson 1984), leaf rust in wheat (Lee & Shaner 1985) and net blotch barley (Cherif & Harrabi 1993). Parlevliet & van Ommeren (1988) used recurrent selection to increase resistance to leaf rust and powdery mildew in barley. By the third cycle of recurrent selection, leaf rust resistance had improved substantially from very susceptible to "sufficiently resistant" (Parlevliet & van Ommeren 1988). All the original parents were considered to be very susceptible. No major genes for resistance were present. The third cycle selections were not immune, but had adequate resistance for protection of barley from leaf rust.

Recurrent selection has been used to improve resistance to several diseases of wheat in Brazil (Beek 1983), purple leaf spot in orchardgrass (Zeiders *et al.* 1984), *Phytophthora* rot in soybean (Walker & Schmitthenner 1984), barley yellow dwarf virus in oat (Baltenberger *et al.* 1988), scab in wheat (Jiang *et al.* 1994) and powdery mildew in rye (Lind & Züchner 1985). It is likely that such resistance is oligogenic or polygenic in nature, and should be durable in agriculture.

In these examples, the breeders were not using the traditional "good sources" of resistance. They used recurrent selection to improve resistance by transgressive segregation. I am not aware of reports of "break down" of polygenic resistance. Worthwhile disease resistance can be achieved without demanding immunity in plants. It is unfortunate that decades of breeding for immunity has resulted in the pessimistic attitude that resistance always breaks down and that breeders will always be one step behind the pathogen.

It is difficult for population geneticists to understand why plant breeders and pathologists have argued emotionally for four decades about the value of this general type of resistance, that Niederhauser *et al.* (1954) termed "partial" and Vanderplank (1963) later called "horizontal". The words horizontal and vertical resistance have invoked hostile reactions in many quarters (Robinson 1996). Even today, there are very few applied breeding programs where population breeding methods are used to increase disease resistance and other important attributes in the production of new cultivars.

In order to adopt population breeding methods for polygenic resistance, it is necessary for breeders to overcome 90 years of bias against polygenic resistance. They must accept that;

- it is not necessary to locate a "good source" of disease resistance;
- disease resistance can be improved to levels far in excess of the parents by population breeding methods, simultaneously with improvements in yield and quality;
- it is rarely necessary for a crop to be immune to disease (in fact, mild disease resistance may be preferable to immunity due to lower selection pressure on the pathogen, and may prevent economic loss in combination with other disease control measures);
- disease resistance does not always break down (in fact, polygenic resistance is likely to be very stable); and
- there is no yield penalty associated with polygenic disease resistance.

The terms vertical and horizontal resistance have been defined and refined for 30 years since Vanderplank (1963) first introduced them. There are many other terms that have been used, but since Vanderplank was the originator of the concept that differentiated the two forms of resistance, Robinson (1996) argues that his terms should take precedence.

Vertical resistance genes belong to the "gene-for-gene" system of plant-pathogen interaction (Robinson 1996). Vertical genes often completely protect plants from disease; however, the protection offered by vertical resistance genes may not be durable. New races of the pathogen, with matching virulence genes, cause vertical resistance to "break down". The resistance gene inside the plant has not changed - it simply is no longer effective as a resistance gene.

The gene-for-gene system is a highly evolved and complex system of disease resistance, almost as complex as the immune system in mammals. In the gene-for-gene system, for every resistance gene in the plant population,

there is a matching virulence gene in the pathogen population. Sooner or later, the pathogen population will respond to the introduction of a vertical resistance gene in a crop variety by developing (under strong selection pressure) high frequencies of its matching virulence gene to overcome the resistance. Vertical resistance is well adapted to wild ecosystems where the host tissue is discontinuous in space and time (for example, in wild cross-pollinating annual grasses), but it is not well adapted to modern agriculture where there are large areas of genetically uniform self-pollinating crops.

Plant breeders normally react to the break down of resistance by introducing new vertical resistance genes. Breeding for vertical resistance is well suited to traditional pedigree and backcross methods of breeding. In many developed countries, such as Australia, the wheat crop continues to be protected from rust diseases by a complex combination of vertical resistance genes. Many developing countries simply cannot afford such costly disease resistance schemes (Robinson 1996).

Horizontal resistance, on the other hand, is presumed

to be effective against all races or strains of the pathogen. In practice this is difficult to prove, but the main feature of horizontal resistance is that it is normally polygenic and durable, although it usually provides incomplete protection and not immunity.

Horizontal resistance is not the "good source" of resistance that plant breeders and pathologists traditionally seek. Horizontal resistance may be increased to useful levels by population breeding methods within an adapted gene pool. Breeding for improvements in horizontal resistance is cumulative. Small additive improvements are accumulated over several cycles of crossing and selection.

In many cases, horizontal resistance is moderately to highly heritable. Resistance to brown spot in lupins was not strong in its effect, but was expressed very consistently across sites and years with high broad sense heritability (Cowling *et al.* 1997). It is possible to breed for resistance, quality and yield at the same time (Cowling 1994). However, it is not possible to breed for horizontal resistance in the presence of vertical genes - horizontal

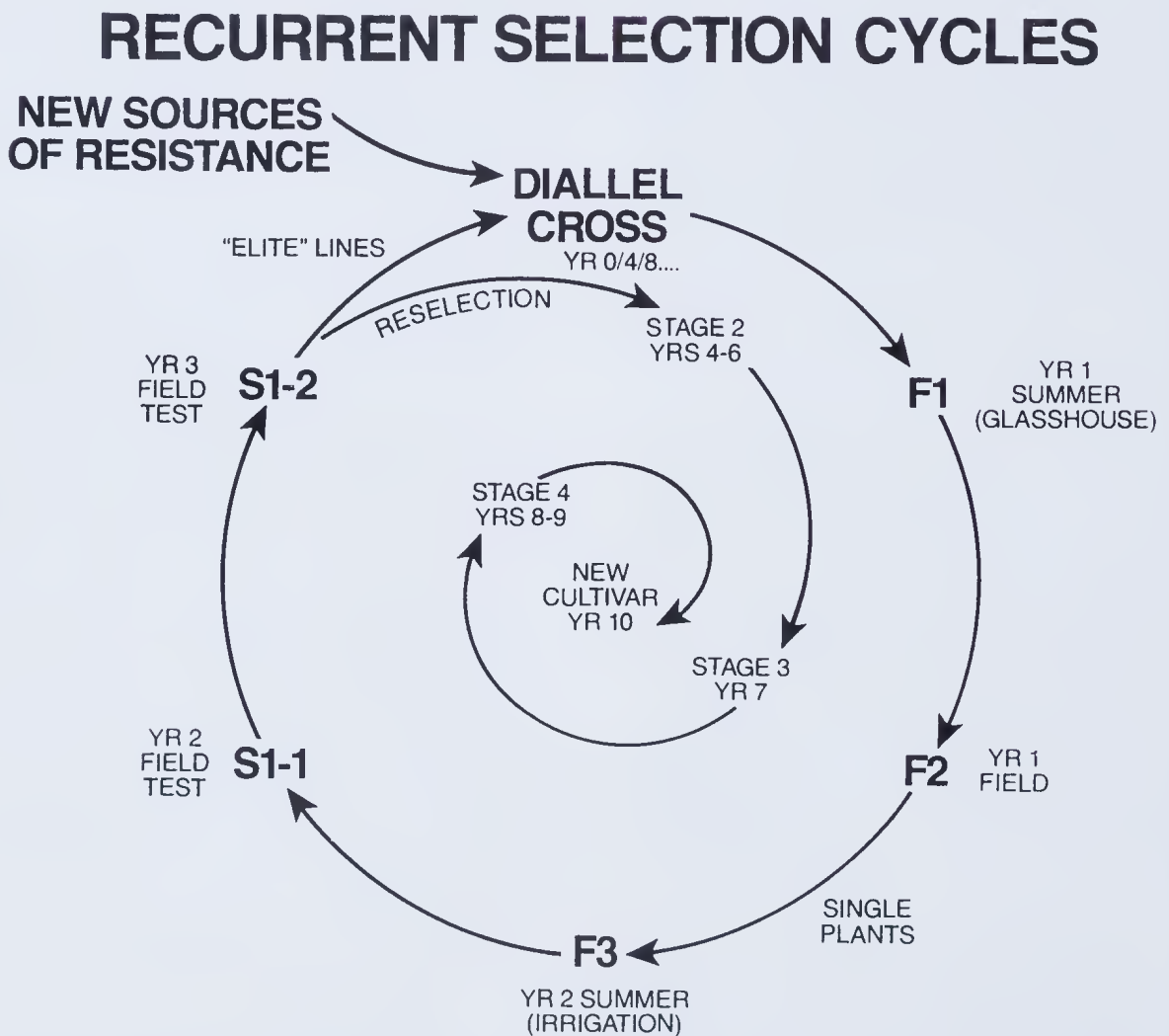


Figure 6. Recurrent selection cycles for improving yield, quality and resistance to brown spot in narrow-leaved lupins in Western Australia. Cycles last 4 years from crossing to selection of F_3 -derived progeny for the next cycle of crossing, during which time two years of field testing is carried out in replicated yield trials. Reselection at the F_3 allows superior lines to be tested for potential release as new varieties.

resistance is masked by vertical resistance genes. Breeding for horizontal resistance must occur in the absence of vertical genes, as John Niederhauser discovered in 1954.

Robinson (1987) discussed procedures for breeding for horizontal resistance against disease. These include: look for moderate, but not strong, resistance in parents; nullify vertical resistance genes (use virulent races of the pathogen); use population breeding methods (recurrent selection); breeding must be "holistic" - against all important diseases, in the target environments; care must be taken to detect "escapes" (susceptible types); select the most resistant off-spring - it is the relative difference in disease levels that is important in early generations.

Stable agriculture may depend on the development of stable disease resistance in crop plants. Population breeding methods may provide the means to develop stable resistance.

Brown spot resistance in lupins: a case history of recurrent selection

Recurrent selection is described in lupins in WA, where closed populations of lupins have been bred with simultaneous improvements in yield, quality and disease resistance.

I have adopted recurrent selection as one of my breeding strategies in lupins. Closed populations undergo early generation selection (as F_2 -derived lines) for yield, disease resistance and quality. Parents are crossed in all possible combinations (a diallel cross) to begin cycle 1 (Fig 6). After quickly proceeding through early generations, including over-summer generations where possible, F_2 -derived lines are tested for yield, disease resistance and quality in replicated field trials in the second and third year. The best of these are selected as parents to begin the next cycle of recurrent selection, and are reselected for further testing and possible release as new varieties.

I have bred lupins for resistance to brown spot by recurrent selection. Brown leaf lesions cause the leaves to fall off prematurely, and if seedlings are attacked early in the season they may be killed. Yield is often reduced by brown spot disease, and it is present in nearly all lupin crops.

Improvements in resistance to brown spot have occurred in a closed population during three cycles of recurrent selection (Fig 7). The vertical axis represents defoliation due to brown spot, measured relative to a control variety Danja which is set at 100%. Along the horizontal axis are the parents used to begin the first, second and third cycle of recurrent selection. All parents were grown together in the same experiment repeated at several sites in WA from 1990 to 1992.

There was a significant decrease in defoliation due to brown spot in the parents of cycles 1 (crossed in 1984), 2 (1988) and 3 (1992) (Fig 7 top). Even more importantly, the best parents in 1992 were more resistant than any of the parents crossed in 1984. Without adding any new resistance genes, resistance is now stronger than in the original parents.

The lines were also selected for yield and other characters during the selection process. Yield increased

gradually from cycle to cycle, with some 1992 parents out-yielding the best of the 1984 parents (Fig 7 centre). Improvements were made to both disease resistance and yield at the same time, in the same breeding material, without adding any new genes. There was no yield penalty for improving disease resistance.

After completing two cycles of recurrent selection in lupins, the following improvements were evident; compared with control cv Danja, brown spot resistance increased 10-14% per cycle, yield increased 5-6% per cycle, Phomopsis resistance increased 30-50% per cycle (this was an added bonus, and unexpected), and average seed alkaloid levels also dropped markedly (Fig 7 bottom). New varieties of lupins in Australia must be lower than cv Danja in seed alkaloids.

As a result of the first cycle of recurrent selection, a new lupin variety with a moderate level of resistance to

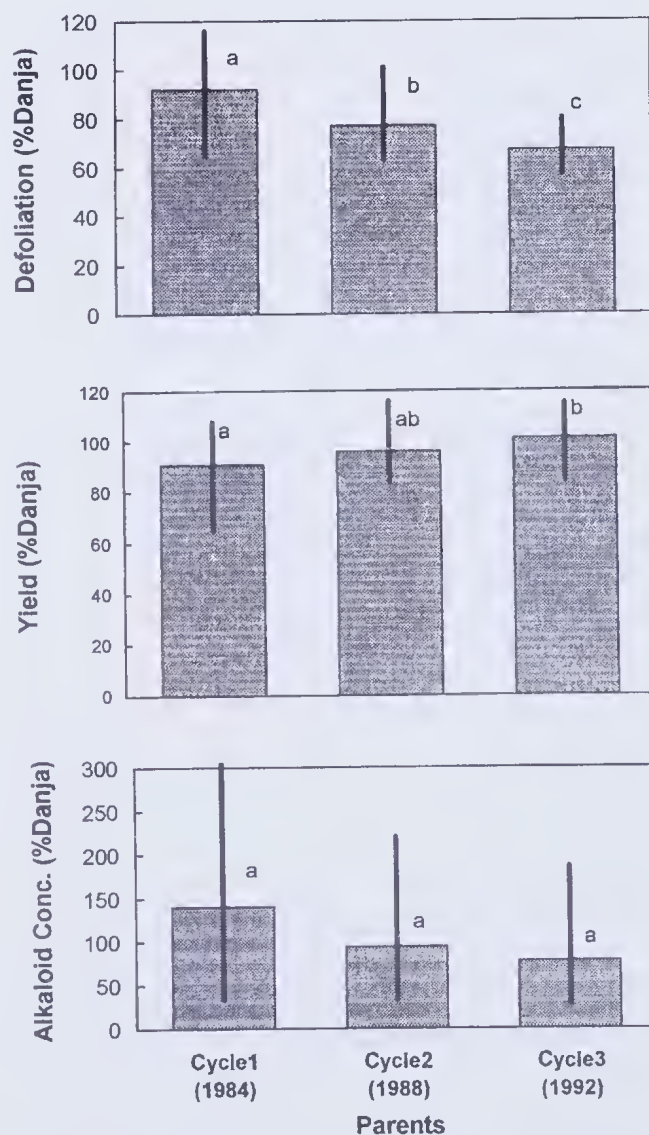


Figure 7. Improvements in resistance to brown spot (top), grain yield (centre) and seed alkaloid concentration (bottom) in parents of the first three cycles of recurrent selection in a closed population of narrow-leaved lupins, compared with control variety Danja (bars represent the range from highest to lowest parent; letters represent significance of difference between cycles at $P = 0.05$). Source: Cowling (1994).

brown spot (cv. Myallie) was released in 1995 (Anon. 1996). Myallie also has strong *Phomopsis* resistance, competitive yield (especially in low rainfall areas of WA where brown spot is most damaging to lupins) and low seed alkaloids. These results are significant on a global scale, because very few breeding programs of self-pollinating crops have released commercial varieties from recurrent selection programs. Until recently, recurrent selection has been restricted to specific research projects (usually PhD research projects) or to breeding of cross-pollinating forage crops.

The future of plant breeding and stable agriculture

There are many strategies that plant breeders can adopt to improve their chances of contributing to the long-term stability of agriculture.

What strategies should plant breeders adopt in order to contribute to stable agriculture in the future?

- 1. Diversify the gene pool:** Invest in the future - create diverse populations in addition to the elite material in the program. Add new genes from new varieties bred elsewhere, or use wild types or landraces from genetic resource collections. Cross into elite lines, and reselect for the quality or adaptation that is required.
- 2. Introduce exotic genes:** interspecific crosses, mutation or genetic engineering. Any source of germplasm is potentially valuable. However, for disease resistance, beware of major genes that may not be durable, or that prevent progress in breeding for polygenic resistance.
- 3. Use population breeding methods:** As demonstrated here, population breeding methods have contributed to increases in disease resistance, yield and quality simultaneously. Disease resistance developed by these methods is usually polygenic and durable.

Crop plants have been evolving since the beginnings of agriculture 10,000 years ago. We may be witnessing a period of "punctuated equilibrium" in the evolution of crop plants, as proposed for evolution in nature (Gould & Eldredge 1993). Wheat and maize have evolved away from their wild relatives in the past 10,000 years due to human intervention (Duvick 1996). Lupins are just beginning to do so. In the Mediterranean region, *L. albus* var. *albus* has been cultivated for thousands of years and is relatively remote from its wild ancestor *L. albus* var. *graeus* in morphology, colour and seed size (Gladstones 1974).

Plant breeders therefore have a great responsibility to lay strong foundations for the future evolution of crop species. The genetic diversity that is now created will become the future gene pool of several new man-made species, which, like wheat or maize, are so remote from their wild ancestors that little introgression from wild relatives will be possible.

I believe that stable agriculture may be achieved if crop rotations are profitable and adapted crop species and varieties are available for growing on each soil and in each climate. Land conservation measures will be an essential component of stability, and another essential component will be the breeding of crop plants with du-

rable disease resistance, low pesticide requirement, high yield and quality, and adaptation to regional environments. Regional adaptation will become more and more important, and the universal crop variety will become a thing of the past. Barley in WA is bred in different gene pools for high and low rainfall environments - a similar situation is likely to develop for lupins over the next several decades.

Breeding programs must have short-term and long-term goals. Given the current push towards privatisation at all levels of Government, it is important to ask: who will take responsibility for the long-term maintenance of genetic diversity in crop breeding? I have indicated that diversity is essential for long-term breeding progress. In Europe and the USA, very few private breeding programs have taken on this role in the case of the common bean, and the gap between the identification of useful characters in exotic germplasm and the transfer to cultivars has widened (Silbernagel & Hannan 1992).

Population breeding methods help to generate genetic diversity, but are still not the favoured procedures in self-pollinating crops. Farmers and plant breeders alike need to ask themselves; what level of disease resistance is sufficient? Do I really need immunity? In most cases, a moderate level of resistance is sufficient, when combined with agronomic or other management packages. Population breeding methods are most ideally suited to long term genetic gains and sufficient lead-time must be allowed to achieve significant gains.

Intuitively, plant breeders will use whatever genetic variation is available to them to improve adaptation of plants to the environment. The future stability of agriculture depends, to some extent, on how successful they are in producing stable varieties, with stable yield, thereby improving the stability of crop rotations, leading to stable profits, and allowing further investment in stable agriculture.

Acknowledgements: This talk and paper would not have occurred without the inspiration of several teachers and mentors in my life who provided the direction for my work, most notably Prof David Gilchrist at the University of California Davis for guidance in research, and Raoul A Robinson for inspiration through his books on plant pathosystems and his optimism for the future of disease resistance breeding. I also thank my employer and colleagues at Agriculture WA, and grain growers in Australia whose funds supported my research through the Grains Research and Development Corporation. Without this assistance, breeding for polygenic resistance in lupins would never have been achieved. I also thank T Khan and M Dracup for valuable comments on this paper.

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Egg laying by thorny devils (*Moloch horridus*) under natural conditions in the Great Victoria Desert

G Pianka¹, E R Pianka² & G G Thompson^{3*}

¹39 Wabank Road, Millersville, Pennsylvania 17551 USA

²Department of Zoology, University of Texas, Austin, Texas 78712-1064 USA

³Edith Cowan University, Joondalup WA, 6027

* to whom reprint requests should be addressed

Manuscript received March 1996; accepted June 1996

Abstract

Three female *Moloch horridus* were recorded in the Great Victoria Desert of Western Australia digging a nesting chamber and laying eggs, in September, October and November, 1995. Two clutches, containing six and seven eggs, hatched after 123–127 days. Ambient temperature in the excavated nesting chamber after hatching was approximately 31 °C. Clutch masses were estimated to be 34.2, 40.9 and 41.7% of the total body mass of the female. The mean mass of neonates was 1.8 g; their mean snout-to-vent (SVL) was 35.7 mm, and their mean total length was 63.8 mm. Neonate *M. horridus* appear to eat their egg shells before digging their way out of the nest chamber. Other published data on egg laying by *M. horridus* are also reviewed.

Introduction

A radiotelemetric study of the movements of *Moloch horridus* was undertaken from mid-September through to early November, 1995. During the course of this study, we were fortunate to observe three gravid females excavate their nest chambers and oviposit. We thus obtained valuable information on pre- and post-oviposition body mass for these three females, allowing estimation of relative clutch mass (RCM). Moreover, two of these nests were monitored over a four month period until hatchlings emerged, and the two nest chambers were excavated.

Methods

Moloch horridus were located by following their spoor in the sandy soil of the Great Victoria Desert (28° 28' S, 123° 36' E). Transmitters were attached to six female and three male *M. horridus*. Lizards were weighed, measured and assigned an alphabetic character from M through U for identification (Table 1). Three adult females, O, P and T, did not lay eggs during the period of observation; N, Q and U did lay eggs. A covered wire enclosure (10 mm galvanised mesh) about 1.5 m in diameter was erected around two of the nests to protect the eggs from predators and to capture the hatchlings when they emerged. A drift fence of flyscreen folded over inwards at the top was erected about a metre outside the covered enclosure to ensure that hatchlings did not escape. The late oviposition date for female U meant that the neonates could not be measured when they hatched, as study at the site would cease in February, as a consequence this nest was not fenced off from predators.

Results and Discussion

Female N, the largest thorny devil which was captured on 16 September, spent three days digging its nesting burrow (Figure 1) at the southern base of a sandridge, and laid its eggs on 19 September, after which it backfilled the nest burrow the next day. The RCM of this female was 34.2% (Table 2). Its post-oviposition mass was 37.5 g and its final mass at the end of the study on 8 November, was 46.5 g; which is a mass gain of 9 g in 50 days or an increase of about 0.5% per day on its post-oviposit body mass. The neonates emerged on 20 and 21 January. The nesting burrow was excavated on 24 January and there were no eggshells in the chamber. The nest chamber (filled with air at 31 °C) was approximately 90 mm high by 120 mm wide and about 150 mm long. The ceiling of this chamber was about 220 mm below ground surface. Hatchlings dug a sloping tunnel through hard-packed sand and emerged at the surface about 300 mm from the nest chamber. They did not dig out through the entrance that had been back-filled by the female. All seven neonates (Figure 2) emerged from the nest through a hole which was about 20 mm in diameter.

Table 1

Dates, sex, size and mass of *Moloch horridus* monitored.

ID	Date of capture	Sex	SVL (mm)	Mass (g) at capture	Mass (g) on 8 November, 1995
M	14 Sept.	Male	82	33.0	(Lost 6 Oct)
N	16 Sept.	Female	105	57.0	46.5
O	20 Sept.	Female	88	38.9	49.5
P	27 Sept.	Female	85	28.5	---
Q	27 Sept.	Female	87	52.0	42.5
R	28 Sept.	Male	76	28.5	30.0
S	4 Oct.	Male	78	32.3	(Lost 12 Oct)
T	5 Oct.	Female	90	51.0	48.5
U	7 Nov.	Female	87	55.0	32.5



Figure 1. Female *Moloch horridus* at the opening of its burrow to the nesting chamber.



Figure 2. Seven neonate *Moloch horridus* shown in hand to indicate their size.

Female Q was captured on 26 September, fitted with a transmitter and released on 27 September. It moved approximately 70 m south over a sandridge and spent several days in early October, digging a nesting burrow into the southern slope of the dune. It laid eggs on 3 October, and backfilled the nest burrow on the same day. The

RCM for female Q was 41.7% (Table 2). The nesting burrow was excavated one day after the neonates emerged (8 February). The nest chamber (filled with air at 30.8 °C) was approximately 80 mm high by 120 mm wide and about 120 mm long. The ceiling of this nesting chamber was about 200 mm below ground surface. Again, the

Table 2

Clutch mass, incubation period and neonate size for *Moloch horridus*.

Parameter	Female N	Female Q	Female U
Date of egg laying	19 Sept.	3 Oct.	12 Nov.
Pre-oviposition body mass (g)	57	52	55
Post-oviposition body mass (g)	37.5	30.3	32.5
Clutch mass (g)	19.5	21.7	22.5
Relative clutch mass (%)	34.2	41.7	40.9
Hatch date(s)	20-21 Jan.	7 Feb.	
Incubation period (days)	123 - 124	127	
Number of hatchlings	7	6	
Mean ($\pm$ SE) mass of hatchlings (g)	1.76 (0.037)	1.9 (0.026)	
Mean ($\pm$ SE) SVL of hatchlings (mm)	35.29 (0.360)	36.17 (0.167)	
Mean ($\pm$ SE) total length of hatchlings (mm)	62.86 (0.738)	64.83 (0.401)	
Total body mass of all hatchlings (g)	12.3	11.4	
Mass lost during incubation (g)	7.2	10.3	

neonates dug a single sloping tunnel to the surface by which all six exited. These neonates did not dig out of the nesting chamber via the entrance backfilled by the female. Again no eggshells were found in this chamber.

The nest burrow of female U was located at the southern base of the same sandridge as those of females N and Q. Female U laid its eggs and backfilled the burrow to its nest chamber on 12-13 November. The RCM for female U was 40.9% (Table 2). When checked on 10 December, this nest had been excavated and predated, probably by a *Varanus gouldii*. However, if incubation time was similar to those of females N and Q, the eggs of female U would not have hatched until mid-March.

There are limited data on oviposition and incubation for *M. horridus* in captivity (White, 1947; Sporn 1955, 1958, 1965) and in natural conditions (Hudson 1977); additional field data are provided by Pianka & Pianka (1970). Clutch size varies from 3 to 10 with a mode of 8 (N = 37; Pianka & Pianka, 1970). Dates of egg deposition by 25 females were as follows; late October (6), early November (8), late November (5), early December (3), and late December (3). In Mandurah, egg laying by captive *M. horridus* was recorded in October and November. White (1947) reports egg laying by *M. horridus* around Coorow from late October to December, and Hudson (1977) reports egg laying in the Whyalla Fauna and Reptile Park, (South Australia), between 30 October and 7 November. Female N laid its eggs a month earlier than Pianka & Pianka's (1970) record for desert specimens, and female Q deposited its clutch a fortnight earlier, lengthening the estimate of the duration of the egg-laying season for desert specimens.

All three female thorny devils chose the southern base of the same sandridge for their nesting burrows, suggesting that this exposure may confer some unknown advantage. We do not know whether hatchlings share the cost of tunnelling out from the nest chamber, or whether the first hatchling does all the work. Sporn (1955, 1965) also reports that neonates emerge from their nesting chamber through a single hole. The lack of egg shells in the nesting chamber suggests that the neonates ate their egg cases. Sporn (1958) also reports no egg cases in the nesting burrow of hatched *M. horridus*. We are

unaware of any evidence to suggest that any other species of squamate consume their own eggshells following hatching; this could add substantially to hatchling body mass and provide neonates with calcium and other materials for early growth. Another unique feature of the nest of *M. horridus* is the large nest chamber, as was also reported by White (1947) and Sporn (1955). We know of no other squamate that lays its eggs into a large air filled chamber that it has excavated. White (1947) reports the entrance tunnel to be about 44 cm with a chamber of approximately 17 cm by 10 cm. Sporn (1955) reports a tunnel of approximately 47 cm leading to a nest about 24 cm below the surface. The placing of the eggs in a chamber, rather than surrounded by sand, may facilitate consumption of eggshells upon hatching. Eggshells of other reptiles being surrounded by sand or soil presumably could not easily be eaten by the hatchling.

Sporn (1965) summarised incubation periods for captive *M. horridus* hatched at Mandurah as ranging from 90 to 132 days, with a mean of 115 days. Hudson (1970) reported that *M. horridus* took between 104 and 110 days to hatch. The 123-124 and 127 incubation days reported for females N and Q respectively are within the range reported by Sporn (1965).

The introduction of a male *M. horridus* into an enclosure that contained a single female in mid-September resulted in a series of attempts by the male to copulate with the female. For a period of 10 to 60 minutes, neither lizard appeared to acknowledge the other's presence. The male then suddenly moved in the direction of the female and rapidly bobbed its head a number of times. When the female remained stationary, the male attempted to mount her from behind, with one hind leg on the ground. The unreceptive female threw the male off her back by a quick longitudinal roll, then moved away from the male.

Acknowledgments: We thank Edith Cowan University for financial support that enabled us to undertake this project. The University of Texas at Austin also helped finance this study. All experimentation was done with the approval of the Animal Ethics Committee of Edith Cowan University and lizards were caught with the approval of the Department of Conservation and Land Management.

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Sea breeze activity and its effect on coastal processes near Perth, Western Australia

G Masselink

Centre for Water Research, University of Western Australia, Nedlands WA 6907

Manuscript received January 1996; accepted October 1996

Abstract

The Perth Metropolitan coastline is exposed to one of the most energetic sea breeze systems in the world, with wind velocities frequently exceeding 10 m s^{-1} . The sea breeze induces a diurnal cycle of nearshore change by causing; (1) an increase in wave height, (2) a decrease in wave period, (3) an intensification of the nearshore currents, (4) an increase in suspended sediment levels and suspended sediment transport, and (5) a modification of the nearshore morphology. The role of sea breeze activity is particularly important along the Perth Metropolitan coastline, because here the sea breeze blows predominantly in a shore-parallel rather than a shore-normal direction. As a consequence, the wind waves induced by the sea breeze are larger, persist longer and approach the coast under a large angle with the shoreline. The alongshore component of the sea breeze and the obliquely-incident wind waves generate strong longshore currents and a northward littoral drift. The sea breeze therefore plays a dominant role in the sediment budget of the Perth Metropolitan coastline.

Introduction

The Perth Metropolitan coastline (Fig 1) is located within the Cape Bouvard to Trigg Island Sector of the Rottneest Shelf Coast (Searle & Semeniuk 1985). This sector is characterized by a complex nearshore bathymetry, and extensive but discrete cells of Holocene deposition in the form of prograded beach ridges and aeolian sand plains. The nearshore geomorphology and bathymetry is dominated by a series of more or less shore-parallel oriented submarine to emergent aeolian ridges that provide extensive sheltering of the mainland coast (Hegge *et al.* 1996).

The mixed tides of the coast are microtidal with a mean spring tidal range of 0.4 m (Department of Defence 1990). Because of the relatively low range of the tide, it is frequently over-ridden by barometric pressure effects on sea level (Clarke & Eliot 1983). The wave climate is dominated by a low to moderate energy, deep water wave regime characterized by persistent south to southwest swell (Davies 1980) and an average offshore significant wave height of 1.5 m (Riedel & Trajer 1978). Closer to shore, the swell is refracted and diffracted by offshore reef systems and greatly attenuated by shoaling across the inner continental shelf. As a result, the inshore wave height is about half of that outside the reef system (Steedman 1977). A highly variable wind wave climate is superimposed on the swell regime, dominated by northwesterly to westerly storm waves during the winter and by the wave field associated with strong south to southwesterly summer sea breezes. Waves in the winter are more energetic than in the summer, inducing a seasonal cycle of beach change with barred, narrow beaches in the winter and wide beaches with a high berm in the summer (Eliot *et al.* 1983).

The coastline of Perth is exposed to one of the most

energetic sea breeze systems in the world (Gentili 1972). Commonly known as the "Fremantle Doctor", the summer sea breeze blows for approximately 60% of the summer days with wind velocities frequently exceeding 10 m s^{-1} (Hounam 1945). The impact of sea breeze activity on the coastal environment is often obscured by the presence of high wave energy levels or large tidal ranges. According to Sonu *et al.* (1973), there has been the tendency to discount its effects on coastal processes. However, along the low wave energy and microtidal Perth Metropolitan coastline, the sea breeze is expected to have a significant impact on the coastal processes in general and on the littoral drift in particular.

Studies by Kempin (1953) and Silvester (1961) indicate the presence of an oscillatory north-south motion of sand along the Perth Metropolitan coastline during the year with a resultant northerly bias. Sand is moving south during the winter as a result of southward-flowing currents generated by northwesterly storms, whereas during the summer the southerly sea breezes induce a northward sediment transport. Such a seasonal pattern of littoral drift is characteristic of the entire Rottneest Shelf region (Searle & Semeniuk 1985).

I report here the results of two field studies carried out at City Beach in Perth to investigate the impact of sea breeze activity on the coastal environment. The temporal scale of my study is considerably shorter than those of previous studies (cited above) as the focus is on the hydrodynamic and morphological changes that take place over the time scale of the sea breeze cycle (one day). I show that sea breeze activity significantly affects nearshore processes along the Perth Metropolitan coastline.

Methods

City Beach is characterized by a steep beachface gradient (7°) and medium-sized sediments (0.3–0.5 mm). Pro-

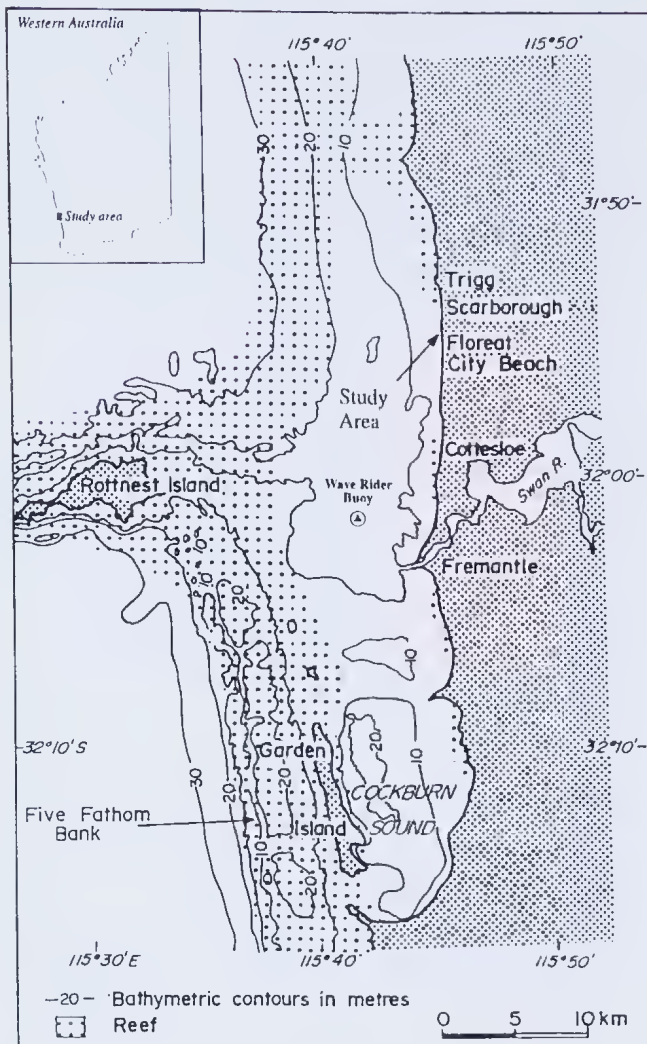


Figure 1. Location map of the Perth Metropolitan coastline and the study site.

nounced beach cusp morphology is typically present with a longshore cusp spacing of around 30 m. During the field surveys, measurements were conducted of; (1) wind speed and direction, (2) nearshore water levels, cross-shore and longshore current velocities and suspended sediment concentrations, and (3) beach morphology. Wind data were collected every five minutes using a standard weather station deployed on the beach berm at a height of 5 m. Hydrodynamic data were sampled continuously at 2 or 5 Hz using an instrument station equipped with a pressure sensor to measure water levels, an acoustic bi-directional current meter and three optical backscatter sensors to monitor suspended sediment concentrations at three different elevations above the sea bed ($z = 0.025, 0.125$ and 0.275 m). The instrument station was deployed in about 1.5 m water depth. The hydrodynamic data were subdivided into sections of 17 minutes and summary statistics were computed. Morphological measurements were made using an extensive array of mild steel pegs (length 1 m and diameter 10 mm) installed on the beachface. The elevations of the tops of the pegs were surveyed every day using a dumpy level. The distance of the top of the pegs to the sand surface was measured hourly using a ruler.

The vertical resolution of the morphological measurements was 1 cm.

The first field survey was conducted in January 1992 and lasted half a day; the energetic surf zone conditions generated by the strong sea breeze (wind velocities $> 10 \text{ m s}^{-1}$) caused frequent toppling of the instrument station and it was not possible to proceed with the measurements during the height of the sea breeze. The hydrodynamic measurements were made in the surf zone under the influence of breaking waves. The second field survey was carried out over six days in March 1995 and included three moderately-strong sea breezes (wind velocities $5\text{--}7 \text{ m s}^{-1}$). Hydrodynamic data were collected under shoaling waves just prior to breaking.

Results

First field survey

Time series of wind speed and direction measured during the first field survey are typical of a sea breeze cycle characterized by weak offshore winds in the morning and early afternoon, and a strong sea breeze starting in the afternoon and continuing into the evening (Fig 2). Wind velocities associated with the land breeze were less than 5 m s^{-1} , whereas they frequently exceeded 10 m s^{-1} during the sea breeze. Such wind speeds are above average, but commonly occur in the summer months on the Perth Metropolitan coastline. The sea breeze started at 14:45 hrs and the change in wind speed and direction was almost instantaneous. The direction of the sea breeze was consistently from the south (180°) and hence the sea breeze was blowing parallel to the shoreline.

The change in the wind climate is reflected in the incident wave field, nearshore currents and suspended sediment concentrations (Fig 2). Prior to the sea breeze, small-amplitude swell with significant wave heights of 0.4 m and zero-upcrossing periods of 7–8 s prevailed. Mean cross-shore currents were negligible ($< 0.05 \text{ m s}^{-1}$) and mean longshore currents flowed in the northward direction with velocities less than 0.1 m s^{-1} . The mean suspended sediment concentration at a distance of 0.275 m above the bed was about 1 g L^{-1} and sediment was only suspended during the passage of large waves in wave groups. The onset of the sea breeze induced almost immediate changes in the nearshore hydrodynamics. The wave height increased, reaching 0.7 m at the end of the field survey. The wave period decreased and assumed a constant value of 4 s within one hour of the start of the sea breeze. Offshore-directed cross-shore currents in the surf zone rapidly increased in strength to 0.16 m s^{-1} and then fluctuated around 0.12 m s^{-1} . The northerly longshore current progressively increased in strength up to 1 m s^{-1} and was still increasing when the survey was abandoned. Sediment was continuously suspended by the waves and the amount of suspended sediment in the water column increased seven-fold to 7 g L^{-1} .

A crude estimate of the longshore suspended sediment transport rate was obtained by multiplying the longshore current velocity by the suspended sediment concentration and integrating the product over the water column and across the surf zone. Before the start of the sea breeze, the northward transport rate was approxi-

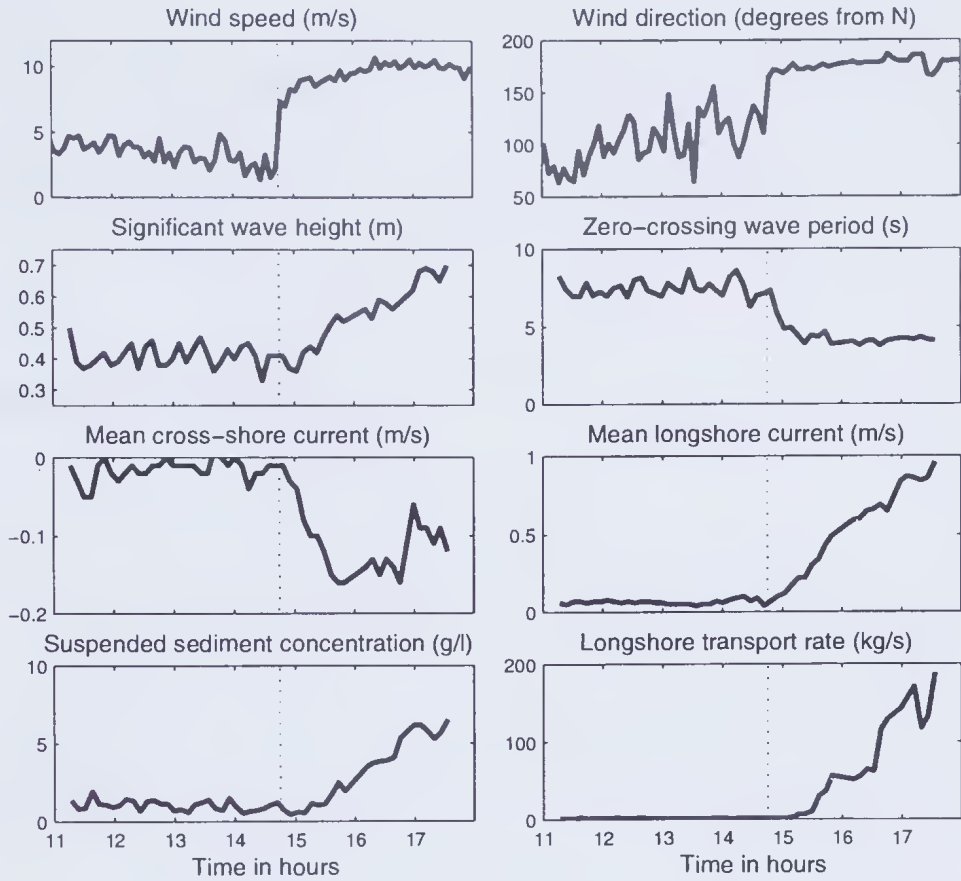


Figure 2. Wind speed, wind direction, significant wave height, zero-crossing wave period, cross-shore current velocity, longshore current velocity, suspended sediment concentration measured 0.275 m above the bed and longshore suspended sediment transport averaged across the surf zone measured on City Beach (23/01/92). The start of the sea breeze is indicated by the dotted line. The sea breeze induces almost instantaneous changes in the nearshore hydrodynamic conditions

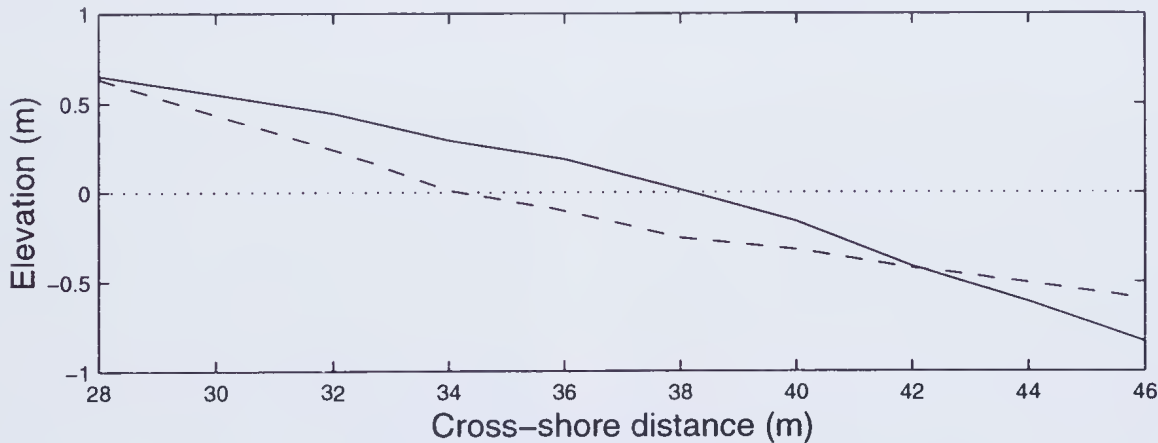


Figure 3. Beachface profile of City Beach (23/01/92) before (solid line; 14:00 hrs) and at the height of the sea breeze (dashed line; 19:00 hrs). During the sea breeze, erosion takes place on the upper part of the beach, whereas accretion occurs low on the beach. The elevation is measured relative to approximately 1 m above mean sea level.

mately 1 kg s⁻¹, but it increased during the sea breeze by two orders of magnitude to 100–200 kg s⁻¹ (Fig 2).

The changes in the hydrodynamic conditions caused by the sea breeze induced an adjustment of the beach morphology; up to 0.4 m of erosion occurred on the up-

per part of the beach, whereas deposition took place on the lower part (Fig 3). The cusp morphology that was present on the beach prior to the sea breeze was completely eradicated. Field observations indicated that the beach cusps reformed overnight, after the sea breeze had subsided.

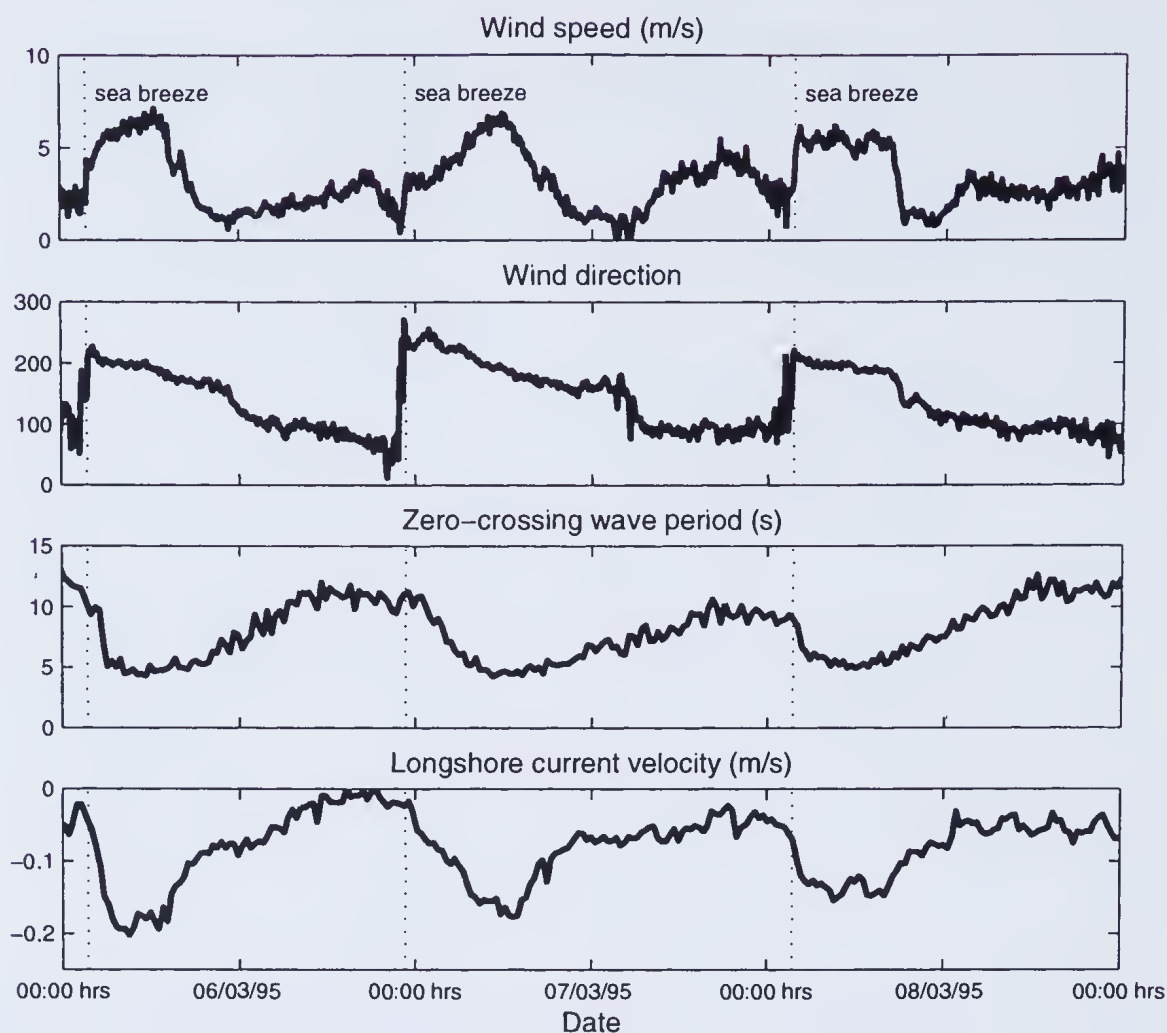


Figure 4. Wind speed, wind direction, zero-crossing wave period and longshore current velocity measured on City Beach (from 12:00 hrs on 06/03/95 to 12:00 hrs on 09/03/95). The start of the sea breezes is indicated by the dotted lines. The effect of the sea breeze on the nearshore hydrodynamic conditions extend a considerable duration after the cessation of the sea breeze.

Second field survey

The second field survey showed essentially the same features as the first, but due to the smaller wind velocities, the hydrodynamic changes induced by the sea breeze were less extreme. Around-the-clock measurements of three successive sea breeze cycles were collected and these enabled the investigation of the recovery period of the wave conditions after the cessation of the sea breeze (Fig 4). Prior to the sea breezes, offshore winds prevailed with speeds of $2\text{--}3\text{ m s}^{-1}$. The start of the sea breezes is indicated by an abrupt change in the wind direction from east to south and an concomitant increase in the wind velocity. All three sea breezes persisted for approximately 7 hours and a relatively constant wind velocity of $5\text{--}7\text{ m s}^{-1}$ was maintained throughout. After the onset of the sea breeze, almost immediate changes occurred to the incoming wave field as indicated by a decrease in the wave period from 10 to 5 s and an increase in the longshore current velocity from insignificant to $0.15\text{--}0.2\text{ m s}^{-1}$. Around 20:45 hrs, the sea breezes stopped. The wind direction gradually shifted back to the east and the wind velocities dropped below 4 m s^{-1} . The wave period started increasing and the longshore current velocity started decreasing as soon as

the sea breeze had subsided. Around 6:00 hrs, nine hours after the end of the sea breeze, the wave period and the longshore current velocity had reached pre-breeze levels.

Energy spectra of the cross-shore current were computed to construct a three-dimensional time-frequency plot to illustrate the change in spectral signature over the second sea breeze cycle (Fig 5). The cross-shore current data were used, rather than the water surface elevation because they show more clearly the short-period wave energy caused by the sea breeze (frequency $> 0.15\text{ Hz}$). The long-period background swell was present in the time-frequency plot in the form of a linear ridge at frequency $0.07\text{--}0.1\text{ Hz}$. The peak period associated with the swell energy was 12 s and remained relatively constant. After the onset of the sea breeze, wind wave energy started to emerge at the high-frequency end of the spectra, indicating peak wave periods of 2.5 s. During the sea breeze, the frequency associated with the wind waves decreased progressively, forming a curving ridge in the frequency-time plot. At the end of the sea breeze (21:00 hrs), the wind wave energy was concentrated around a frequency of 0.25 Hz , indicating a peak period of 4 s. After the sea breeze had subsided, the wind wave energy gradually decreased, but remained significant.

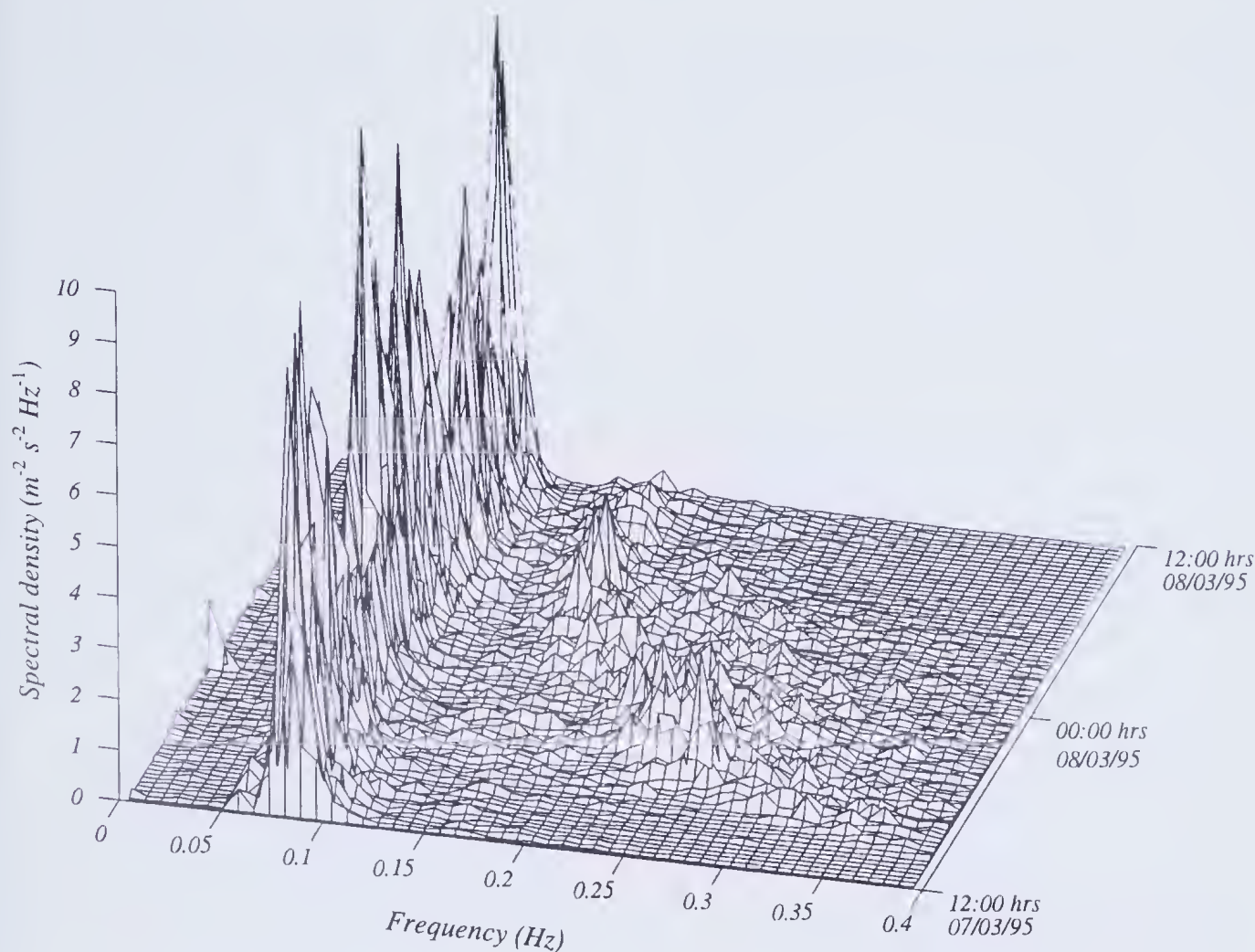


Figure 5. Frequency-time plot of spectra of the cross-shore current velocity measured on City Beach (from 12:00 hrs on 07/03/95 to 12:00 hrs on 08/03/95). The background swell is represented by the linear ridge around 0.08 Hz, whereas the wind waves are indicated by the curving ridge at 0.15–0.4 Hz.

The frequency associated with the wind wave energy decreased to 0.15 Hz, merging with the swell energy. Fifteen hours after the cessation of the sea breeze (12:00 hrs 08/03/93), there was still some wave energy present that was generated by the sea breeze in the nearshore zone. This implies that the effect of the sea breeze on the nearshore hydrodynamics may be continuous during the sea breeze season (summer).

The three sea breezes monitored during the second field survey induced changes to the beach morphology (Fig 6). Pronounced beach cusp morphology remained present on the beach, but during the sea breeze, erosion took place on the cusp horn and accretion occurred in the cusp embayment. Consequently, the beach cusp morphology became less pronounced. No sediment exchange was observed between the upper part of the beach and the nearshore zone, since morphological changes involved a shore-parallel redistribution of sediment over the beach cusp system.

Discussion

The findings of two field surveys, aimed at investigat-

ing the impact of sea breeze activity on nearshore processes, are similar to those of Sonu *et al.* (1973), the only other study into sea breeze effects. The sea breeze results in; (1) an increase of the wave height, (2) a decrease in the wave period, (3) an intensification of the nearshore currents, (4) an increase in suspended sediment levels and suspended sediment transport, and (5) a modification of the nearshore morphology. Due to the predominantly longshore component of the sea breeze, the nearshore hydrodynamics are affected long after the sea breeze has ceased to blow. Sonu *et al.* (1973) refer to this as the "afterglow effect". Both the strength and consistency of the sea breeze, and the afterglow effect contribute to the important role that the sea breeze plays on the nearshore processes along the Perth Metropolitan coastline.

The role of sea breeze activity in this region is particularly important because the sea breeze blows predominantly in a shore-parallel direction. The seaward extent of the sea breeze is usually 50–100 km (Hsu 1988; Simpson 1995) and consequently, the generation of wind waves by an shore-normal sea breeze is limited by the fetch length, restricting both the height of the wind waves and the duration over which the waves influence

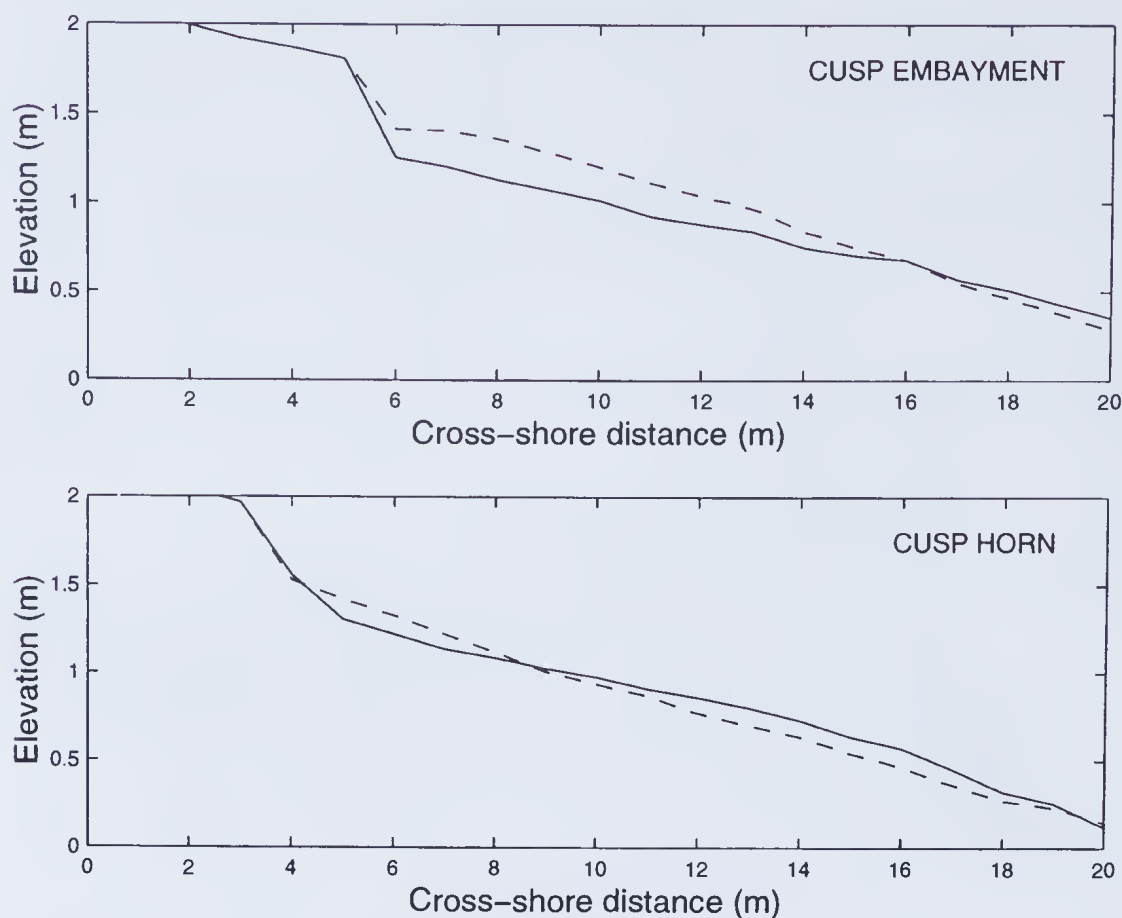


Figure 6. Beachface profile of the cusp embayment and the cusp horn on City Beach (08/03/95) before (solid line; 14:00 hrs) and after (dashed line; 21:00 hrs) the sea breeze. During the sea breeze, erosion of the cusp horn is accompanied by accretion in the cusp embayment. The elevation is measured relative to approximate mean sea level.

nearshore processes. For a shore-parallel blowing sea breeze, the fetch is virtually unlimited and given sufficient duration of the sea breeze, the wind wave field can attain its maximum energy level and develop into a "fully-developed" sea. In addition, wind waves may continue to arrive at the coastline long after the sea breeze has subsided. Finally, the obliquely-incident wind waves and the longshore wind stress may induce strong longshore currents that affect littoral transport.

The sea breeze induces a diurnal cycle of beach change by causing erosion of the upper part beach and/or planation of beach cusp morphology. These changes are reversible in that the beach is usually restored to its pre-breeze state after the cessation of the sea breeze. On the larger temporal and spatial scale, the dramatic increase in the longshore sediment transport caused by the sea breeze is important. Masselink & Pattiaratchi (in press) and Pattiaratchi *et al.* (in press) estimate that along the Perth Metropolitan coastline, the annual longshore transport driven by the sea breeze is approximately 100,000 m³. This estimate corresponds to calculations of sediment accumulation at the southern side of Trigg Island (Perth) at the end of the summer. It is apparent that the sea breeze must play a dominant role in the sediment budget of the coastline around Perth. For example, a significant proportion of the sediment required for shoreline progradation of cusped forelands such as Becher

Point and Rockingham (Woods & Searle 1983), Whitfords Cusp (Semeniuk & Searle 1986), Jurien (Woods 1983), and other types of coastal landforms such as tombolas and salients (Sanderson & Eliot 1996) is probably contributed by the littoral drift induced by sea breeze activity.

Acknowledgments: The author would like to thank all the people that have assisted in the collection of the field data reported here, in particular I Eliot, B Hegge and C Pattiaratchi. Comments by the two anonymous reviewers are also acknowledged. This paper has Centre for Water Research reference ED1115GM.

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A genetic perspective on the specific status of the Western Rock Lobster along the coast of Western Australia – *Panulirus cygnus* George 1962 or *P. longipes* A Milne-Edwards 1868?

A P Thompson

Department of Zoology, University of Western Australia, Nedlands WA 6907

Manuscript received July 1996; accepted October 1996

Abstract

Panulirus longipes is widespread throughout the Indo-west Pacific and *P. cygnus* is restricted to the coast of Western Australia. Controversy regarding their discreteness has continued since the early 1900's based on the lack of morphological differences and the potential for gene-flow between these species. Allozyme variation indicates a discreteness of *P. cygnus* and *P. longipes* along the coast of Western Australia. Unique alleles were found at the PGM locus in *P. longipes*. At 3 other loci (*EST*, *GPI*, and *MDH-2*) the probabilities that these individuals came from a population which was genetically common to *P. cygnus* were extremely low (1.4×10^{-4} , 4.9×10^{-3} , and 2.2×10^{-6} respectively). Nei's (1978) unbiased measure of genetic identity separated *P. cygnus* from *P. longipes* at 0.759. The evidence supports genetic discreteness of the two species along the coast of Western Australia and thus supports the views of George (1962) that *P. cygnus* is a valid species.

Introduction

The Western Rock Lobster, *Panulirus cygnus*, inhabits the west coast of Australia approximately from Cape Leeuwin (34° 22'S) to North West Cape (21° 45'S). Seven other species of rock lobster also inhabit the west coast of Australia, but this zone is mainly occupied by *P. cygnus* with only minimal overlap with other species. *Jasus novaehollandiae* (Holthuis 1963, cited by Holthuis 1991) is sympatric with *P. cygnus* at the southern end of the range, while at the northern end there is an overlap with several tropical species, *P. versicolor* (Latreille 1804, cited by Holthuis 1991), *P. ornatus* (Fabricius 1798, cited by Holthuis 1991), and *P. penicillatus* (Olivier 1791, cited by Holthuis, 1991). Occasional specimens of *P. longipes* have been recorded in this zone. The two other species are *P. polyphagus* (Herbst 1793, cited by Holthuis 1991) which occurs in the muddy water near Derby, and *P. homarus* (Linnaeus 1758, cited by Holthuis 1991) which inhabits turbid waters off the Pilbara coast (see Gray 1992).

Conjecture regarding the discreteness of *P. cygnus* has continued since 1912 (see Gray 1992). Some scientists believed that there were insufficient morphological differences (Glauert 1936; Sheard 1949; Chittleborough & Thomas 1969) as well as a lack of evidence of genetic isolation to warrant ranking *P. cygnus* as a distinct species. Rather, it was suggested that *P. cygnus* was part of a more widespread population of *P. longipes*, which is an Indo-west Pacific species (see Holthuis 1991). The subspecies *P. longipes longipes* is the western form, occurring from East Africa to Thailand, the Philippines and Indonesia. Occasional specimens of *P. l. longipes* are found along the coast of Western Australia within the zone of *P. cygnus*. The eastern subspecies *P. l. femoristriga* inhabits Japan, the Moluccas, New Guinea, Eastern

Australia, New Caledonia, and Polynesia (Holthuis 1991).

Recognition of the western rock lobster as a distinct species has significant implications for the fishing industry. If it were part of the more widespread species, *P. longipes*, as suggested by Glauert (1936), Sheard (1949), and Chittleborough & Thomas (1969), then lobsters caught on the West Australian coast may have come from larvae drifting with ocean currents from elsewhere in the Indian and Pacific Oceans. Thus, protecting the breeding population on the coast of Western Australia may not be such a crucial management strategy. However, recognition of the western rock lobster as a discrete species *P. cygnus*, restricted to the waters off Western Australia, dictates that the fishery be managed accordingly.

Allozyme electrophoresis is a useful tool for distinguishing populations and species. One of the implications of a discrete population is that there is no gene-flow between it and other populations. Absence of gene-flow allows genetic differences to accumulate over generations through natural selection, random genetic drift, and mutation (Wallace 1981). This can result in speciation. Usually, distinct populations and/or species will show genetic differences (Altukov 1981; Johnson *et al.* 1993; Shaklee 1983). Intraspecific populations are distinguished in the most part by different frequencies of shared alleles, while species are distinguished by fixed allelic differences (Altukov 1981). Thompson *et al.* (1996) found no evidence of latitudinal genetic variation among populations of the western rock lobster from Garden Island to Shark Bay. The average F_{ST} among 5 sites over the 9 polymorphic loci studied was a very low 0.0002, which is consistent with current interpretations that the western rock lobster is a single panmictic population (see Thompson *et al.* 1996). The aim of this study was to investigate the genetic discreteness of *P. cygnus* and *P. longipes* along the coast of Western Australia.

Table 1

Enzymes and electrophoretic buffers used to study genetic variation in *P. cygnus* and *P. longipes*. Buffer recipes are given in Hillis & Moritz (1990).

Enzyme	E.C. number	Locus abbreviation	Buffer
Arginine phosphokinase	2.7.3.3	APK	TC8
Esterase	3.1.1.-	EST	TC8
Glucose phosphate isomerase	5.3.1.9	GPI	LiOH
Leucylproline peptidase	3.4.-.-	LPP	TC8
Leucylglycylglycine peptidase	3.4.1.3	LGG	TC8
Malate dehydrogenase	1.1.1.37	MDH-1, MDH-2	TM
Mannosephosphate isomerase	5.3.1.8	MPI	TC8
6-Phosphogluconate dehydrogenase	1.1.1.44	6PGD	TM
Phosphoglucomutase	2.7.5.1	PGM	TM
Valylleucine peptidase	3.4.-.-	VLP	TC8

Materials and Methods

A leg from each of 455 adult rock lobsters (*P. cygnus*) was collected during 1994. Rock lobsters were collected at commercial depots at 5 locations; Garden Island (n=84), Two Rocks (n=81), Geraldton (n=97), Southern Abrolhos (n=99) and Shark Bay (n=94). These samples were frozen immediately in liquid nitrogen before being transferred to a freezer at -70°C. Tissue samples (muscle) from three *P. longipes longipes* were collected during 1995, also from a commercial depot. The *P. longipes* specimens were characterised by the presence of pale spots on the legs. These specimens were caught off Shark Bay, within the zone of *P. cygnus*. They were frozen immediately in liquid nitrogen and later stored at -70°C.

Ten enzyme systems representing 11 loci were scored in both *P. cygnus* and *P. longipes* (Table 1). Electrophoretic



Figure 1. Isozyme formation of PGM showing the fixed allelic differences of the *P. longipes* specimens (positions 2-4) compared to *P. cygnus* (positions 1, 5-8). Individual genotypes from left to right are: 22, 34, 34, 33, 22, 22, 22, 22.

procedures are described in more detail by Thompson *et al.* (1996).

Expected genotypic frequencies at each locus were calculated using BIOSYS-1.7 (Swofford & Selander 1981). The genotypic frequencies at each locus from the pooled *P. cygnus* population (since Thompson *et al.* 1996 found no evidence of genetic subdivision) were used as probability estimates for the observed genotypic frequencies of the *P. longipes* individuals. The expected probability of a *P. longipes* individual having a particular genotype was equal to the expected frequency of that genotype occurring in the *P. cygnus* population.

The genetic differentiation among populations was examined using BIOSYS-1.7 (Swofford & Selander 1981). Clustering was performed based on the methods of Nei's (1978) unbiased genetic identity.

Results

One locus, PGM, showed unique alleles and genotypes between the 2 groups (Figure 1, Table 2). At ten loci, the 3 *P. longipes* specimens had alleles common

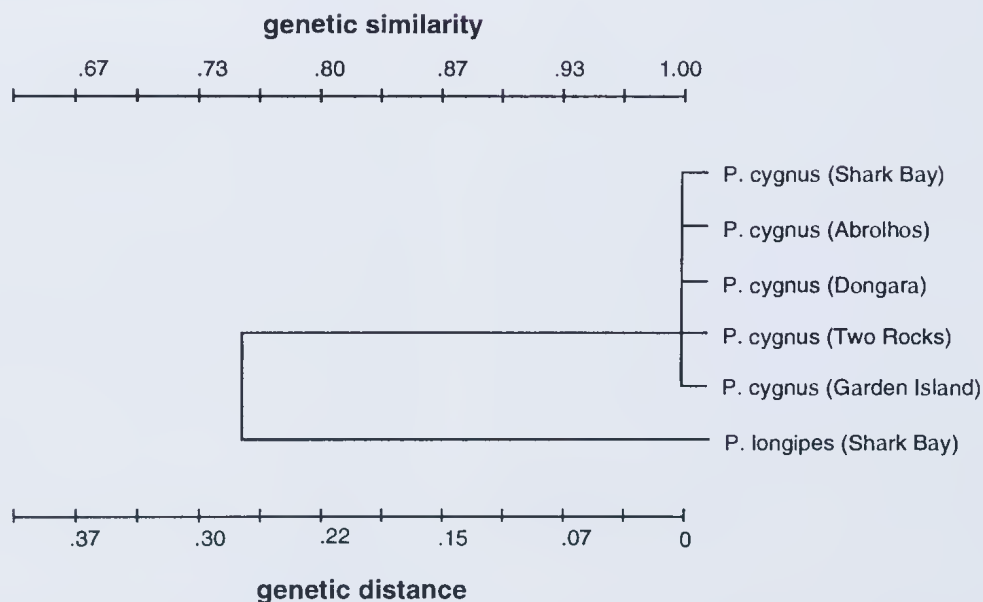


Figure 2. Dendrogram based on Nei's (1978) unbiased genetic identities of *P. cygnus* and *P. longipes* caught off the coast of Western Australia.

Table 2

Genotypic classes of *P. cygnus* with their associated observed frequencies, and the individual genotypes scored for each *P. longipes* specimen with the associated probabilities that these animals came from a population that was genetically common to *P. cygnus*. N is sample size.

<i>P. cygnus</i> (N = 455)			<i>P. longipes</i> (N = 3)		
Locus	Genotypes	Frequency	Locus	Genotypes	Probability
APK	2-2	1	APK	2-2, 2-2, 2-2	1
EST	1-1	0.024	EST	1-1, 1-1, 1-1	1.4 10^{-4}
	1-2	0.229			
	1-3	0.747			
GPI	1-1	2.198 10^{-3}	GPI	2-2, 2-2, 2-2	4.9 10^{-3}
	1-2	4.396 10^{-3}			
	1-3	8.791 10^{-3}			
	2-2	0.1692			
	2-3	0.4132			
	3-3	0.4022			
IDH	2-2	1	IDH	2-2, 2-2, 2-2	1
LGG	2-2	1	LGG	2-2, 2-2, 2-2	1
LPP	1-2	0.0202	LPP	2-2, 2-2, 2-2	0.9415
	2-2	0.9801			
MDH-1	1-2	6.593 10^{-3}	MDH-1	2-2, 2-2, 2-2	0.9609
	2-2	0.9868			
	2-3	6.593 10^{-3}			
MDH-2	1-1	1.32 10^{-2}	MDH-2	1-1, 1-1, 1-1	2.2 10^{-6}
	1-2	0.1165			
	2-2	0.8615			
	2-3	8.80 10^{-3}			
MPI	2-2	0.9956	MPI	2-2, 2-2, 2-2	0.9869
	2-3	4.3956 10^{-3}			
PGM	1-2	1.538 10^{-2}	PGM	3-3, 3-4, 3-4	0
	2-2	0.9846			
VLP	1-2	1.32 $\times 10^{-2}$	VLP	2-2, 2-2, 2-2	0.8683
	2-2	0.9540			
	2-3	3.330 10^{-3}			

to both species. However, the probabilities of them coming from a population which was genetically linked to *P. cygnus* were extremely small at the *EST*, *GPI*, and *MDH-2* loci (Table 3). At the other 7 loci (*APK*, *IDH*, *LGG*, *LPP*, *MDH-1*, *MPI*, and *VLP*) the 3 *P. longipes* specimens shared alleles, with no evidence of differences between the 2 groups. Nei's (1978) genetic identity cluster analysis clearly separated the *P. longipes* specimens from all *P. cygnus* populations at 0.759 (Figure 2).

Discussion

Even though only 3 individual *P. longipes* were used in this study, it is clear that these animals came from a population that is not genetically linked (*i.e.* there is no gene-flow) to *P. cygnus*. *PGM* was the definitive locus for this conclusion with completely unique alleles and genotypes observed in all 3 *P. longipes* specimens. Even if there was only a small amount of gene-flow between the 2 groups, one would expect rare genotypes (or at least alleles) to occur in 455 animals. This was not the case. Furthermore, Nei's (1978) unbiased estimate of genetic identity separated the 2 species at 0.759. In a study of the

freshwater crayfish genus *Cherax*, 6 species were separated with genetic identities ranging from 0.92 to 0.53 (Austin & Knott 1996). The electrophoretic results here provide the evidence of genetic isolation between *P. cygnus* and *P. longipes* along the coast of Western Australia that was lacking at the time of Chittleborough & Thomas (1969).

Phillips (1981) reported that larvae of *P. cygnus* are transported offshore through a combination of behavioural adaptations resulting in the early phyllosoma being at the surface at nights, and surface currents (summer pattern of offshore wind drift) during the early stage of their life-cycle. Mid to late stages are entrained within mesoscale eddies and gyres up to 1000 km offshore. Final stages are returned by a change in behaviour (spending more time at greater depth) in conjunction with the deeper onshore flow. Pollock (1992) presumed from oceanographic characteristics that the larval pool of *P. cygnus* off the coast of Western Australia resulted in separation and ultimately in speciation of this group. The genetic evidence supports the notion that *P. cygnus* is genetically isolated from *P. longipes* along the coast of Western Australia.

However, larval transport processes occasionally result in larvae being moved long distances. The *P. longipes* collected for this study presumably came to the coast of Western Australia via larval transport rather than by juvenile migration. This shows the possibility for gene-flow between *P. cygnus* and *P. longipes*. Phillips *et al.* (1980) proposed that near-adult specimens of *P. cygnus* with pale spots on their legs (characteristic of specimens of *P. longipes* from type locality of Zanzibar) were in fact hybrids due to gene-flow from the north. More likely, these individuals were foreign larvae which managed to metamorphose to become juveniles.

The foreign *P. longipes* specimens negate the hypothesis of Pollock (1992) that larvae from each species only metamorphose into the settling puerulus stage when they experience physical, and/or chemical cues native to endemic environments. It is more probable that species are separated due to physical isolation (*i.e.* entrainment of larval pools) rather than due to the failure of foreign larvae to metamorphose. Larvae of *P. longipes* may occasionally be transported and even settle in the waters off Western Australia, but the genetic evidence supports a lack of significant transfer of genes between these groups.

Acknowledgements: Thanks to the Fisheries department of Western Australia for facilitating this project, and to M Johnson and K Whitaker for valuable comments on the manuscript. This project was funded by the Zoology Department of the University of Western Australia.

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Roost selection by the lesser long-eared bat, *Nyctophilus geoffroyi*, and the greater long-eared bat, *N. major* (Chiroptera: Vespertilionidae) in *Banksia* woodlands

D J Hosken

Department of Zoology, University of Western Australia, Nedlands WA 6907

Manuscript received April 1996; accepted July 1996

Abstract

Radiotelemetry was used to track eight *Nyctophilus geoffroyi* and three *N. major* to roosts in *Banksia* woodland, on the Swan Coastal Plain south of Perth, intermittently between January and August 1995. All roosts were found in large or dead trees and bats were never captured more than 1.2 km from their roosts. Twenty two roosts were identified in six species of trees. Both species of bat changed roosts regularly, and were always found to roost alone. *N. geoffroyi* showed a strong preference for roosts in dead *Banksia* trees, although they also roosted in *Melaleuca* trees during storms. The differential use of the two tree species by *N. geoffroyi* may relate to water harvesting differences between the two types of tree, and to temperature differences between roosts found in each tree species; roosts in *Melaleuca* trees stay dry but are much colder than roosts in *Banksia* trees. *N. major* were tracked to *Eucalyptus rudis* and *Melaleuca rhaphiophylla* trees, but only one roost was actually located. Stands of forest containing dead trees may be necessary for the persistence of both species.

Introduction

Roost sites are a critical resource for bats, providing shelter, protection, mating and hibernation sites (Kunz 1982). It has been argued that roost availability is, or may become, a limiting resource for many bat species (Taylor & Savva 1988).

While a number of studies have investigated the use of roosts by eastern Australian bats (e.g. Taylor & Savva 1988; Lunney *et al.* 1988, 1995), little is known about the roosts used by forest bats in Western Australia. This is particularly true for *Nyctophilus geoffroyi*, for which no detailed account of roost use has been published.

The lesser long-eared bat, *N. geoffroyi* is a small (5.5–8.0 g) vespertilionid bat. Its diet includes lepidopterans, coleopterans, hymenopterans, dipterans and orthopterans (Vestjens & Hall 1977). *N. geoffroyi* is known to forage by gleaning and is able to exploit prey generated noise, including acoustic signals, to locate prey (Grant 1991; Hosken *et al.* 1994). These bats are found throughout Australia, with the exception of Cape York Peninsula (Hall & Richards 1979), although their taxonomy may be more complex than is currently recognised (N L McKenzie *pers. comm.*; H Parnaby *pers. comm.*). *N. geoffroyi* is reported to roost in trees, in hollows and under bark, and also roosts in buildings (Lumsden & Bennett 1995; Reardon & Flavel 1991). These bats usually roost alone (Lumsden & Bennett 1995; L Lumsden *pers. comm.*) or in small maternity colonies of generally less than 30 individuals, although one colony of about 200 *N. geoffroyi* has been reported (Reardon & Flavel 1987).

Less is known about the biology of *N. major* (also known as *N. timoriensis*). It is widely distributed but

uncommon throughout southern Australia, although the presence of distinct geographic forms indicate that a species complex may be present (Parnaby 1995). It is about twice the size of *N. geoffroyi*, weighing between about 11 to 20 grams. *N. major* is thought to roost alone or in pairs in tree hollows, but even this is uncertain (Richards 1991).

This study primarily aimed to investigate roost selection by *N. geoffroyi* in *Banksia* woodlands on the Swan Coastal Plain south of Perth. In addition, the fortuitous capture of three *N. major* provided an opportunity to investigate roosting in this species.

Methods

This study was carried out at the Harry Waring Marsupial Reserve, Wattleup (approximately 32° 15' S, 115° 50' E) from January to August 1995. The reserve is small, approximately 250 hectares, and is predominantly low open woodland on Bibra Sands. It includes a mixture of *Eucalyptus rudis*, *E. gomphocephala*, *E. marginata* and *Melaleuca preissiana* and *M. rhaphiophylla*, but is dominated by *Banksia* woodlands (*Banksia attenuata* and *B. menziesii*), with a variable understory (for further description see Hosken & O'Shea 1994).

Bats were captured in mist-nets set in woodlands and were fitted with small radio-transmitters (Titley Electronics) with 8–12 cm flexible wire antennas and an expected battery life of about 8 days. Transmitters weighed between 0.7 and 1.1 g, which represents 11–17% of the mean body weight of the *N. geoffroyi* captured during this study (less than 9% of the body weight of *N. major*). This is less than the weight of the two foetuses that female *N. geoffroyi* carry during late pregnancy (unpublished data), and is proportionally less than the mass of transmitters carried by bats in other studies (e.g. Lunney *et al.* 1995; 12–19% of body mass). In trials with

three captive *N. geoffroyi*, transmitters did not appear to adversely affect the bats behaviour or mobility, and transmitters were shed in 6–15 days. Bats fitted with transmitters in this study did not lose weight over the 4–6 days that they carried transmitters, which also indicates that transmitters had no obvious adverse effects.

Transmitters were attached to the dorsal fur between the shoulder blades using rapid-set cyanoacrylate glue, with the antenna projecting posteriorly. Diurnal roosts were then located by radiotelemetry, with radio-signals from transmitters received using a receiver and directional 'h-frame' antenna (Biotelemetry, SA). Roost location was usually confirmed by sighting the bat or the transmitter antenna.

The following roost characteristics were recorded; tree species and whether it was alive or dead, the diameter at breast height (DBH), the roost height, the direction it faced and distance from last sighting of the bat. Distances were either measured directly or calculated using a map marked with 100 x 100m grids. Later, when roosts were vacant, temperature fluctuations inside and outside each roost were recorded during the course of a day. Each roost was visited once each hour from 9am till 5pm and the temperature in the roost (T_r) and the ambient temperature (T_a) just outside the roost were recorded using a Radio Spares type-K thermocouple meter and thermocouple.

Statistics were mainly performed using the Statview + SE statistical package, and data are presented as means with $\pm$ standard error, unless stated otherwise.

Results

Eight (four male, four female) *N. geoffroyi* and three (two male, one female) *N. major* were tracked over a total of 42 days during 1995. *N. major* were tracked in January and February, while the *N. geoffroyi* were tracked intermittently from April to August. During this time *N. geoffroyi* begins mating; the sperm is stored until about October, when pregnancy is initiated (Hosken unpublished data). The *N. major* were each tracked for four days and nights, and six roost trees were identified. Two *N. geoffroyi* lost transmitters and one was killed by an owl on the first night. The other five were tracked for

Table 1

The tree species in which bats were found to roost. (Dead or alive refers to the tree)

Tree spp	<i>N. major</i>	<i>N. geoffroyi</i>
<i>Banksia attenuata</i>	0	6 (all dead)*
<i>Banksia menziesii</i>	0	2 (all dead)*
<i>Eucalyptus rudis</i>	3 (2 alive but burnt, 1 dead)	1 (dead)
<i>Eucalyptus marginata</i>	0	1 (dead)
<i>Melaleuca pressiani</i>	0	4 (all alive)
<i>Melaleuca rhaphiophylla</i>	3 (all alive)	0

* Two other roosts were located in dead banksia; however, the species could not be determined.

Table 2

The diameter at breast height (DBH) and roost height of trees in which *N. geoffroyi* roosts were found (mean $\pm$ SE).

Tree	DBH	roost height
<i>Banksia attenuata</i>	0.38m (± 0.1)	1.85m (± 0.55)
<i>Banksia menziesii</i>	0.25m (± 0.13)	0.85m (± 0.15)
<i>Eucalyptus rudis</i>	0.38m	2.9m
<i>Eucalyptus marginata</i>	1.19m	5.1m
<i>Melaleuca pressiani</i>	0.9m (± 0.1)	2.13m (± 0.52)

four to six days each, allowing 15 roosts to be identified. An additional *N. geoffroyi* roost was found while searching for a *N. major*.

N. geoffroyi changed roosts frequently (mean number of days that each roost was occupied was 1.13 ± 0.15) and were predominantly found roosting in dead *Banksia* trees, under bark that had come away from the tree trunk to form a loose fitting sleeve. (Fig 1, Table 1). *N. major* were found to roost in Paperbark trees or Flooded gums and occupied each tree for 1.83 ± 0.48 days.

N. geoffroyi tended to move roosts on a daily basis, except for one bat which was found in the same roost on 3 consecutive days during a storm; this roost was in a Paperbark tree (*Melaleuca preissiana*). The only times these trees were used as roosts by *N. geoffroyi* was during storms or when it was raining (4 bats on 6 days; 6 out of 6 occasions; sign test $P = 0.016$). Roosts were always under bark. Interestingly, these were the only live trees in which *N. geoffroyi* roosts were found, and no bats were found to be roosting in *Banksia* trees when there had been rain overnight. *N. geoffroyi* were located in roosts on 16 occasions and were always alone. Roosts tended to be close to the ground (1.93 ± 0.36 m), but average roost height varied with the species of tree as did the DBH of trees in which bats roosted (Table 2). The majority of roosts were either on the north or west face of trees or were in direct afternoon sun (9 of 14; note that the roost used on three consecutive days was only counted once)

Only one of six *N. major* roosts was located. This was in a fissure within a branch of a burnt-out, dead *E. rudis*. This branch was shared with an unmarked *N. geoffroyi*, although these bats were not in the same fissure. Other roosts, in large *Melaleuca rhaphiophylla* trees, were inaccessible, but two *N. major* were located in the same trees for three and four consecutive days respectively.

While *N. geoffroyi* were sometimes captured a substantial distance from where they were subsequently found to roost (850–1200 m maximum), the roosts used by an individual were generally much closer to each other (mean distance roost to roost = 194 ± 57 m) suggesting some area fidelity (Fig 2). A Student's t-test comparison of the mean distance between the point of capture and the roost location on the day after capture, and the mean distances moved between roosts, revealed that the difference was statistically significant (unpaired t_{15} value = 3.33, $P = 0.0046$). There was no significant difference between the sexes in the distances moved between roosts or in the distances between point of capture and subsequent roost location (two tailed unpaired Student's t-test comparison, $P > 0.32$ for each comparison).



Figure 1. Typical *N. geoffroyi* roost found in dead *Banksia* tree. Roost (marked with arrow) was 0.8 m above ground. Width of central branch was 0.32 m.

There was a significant and positive relationship between T_a and T_r in both *Banksia* and *Melaleuca* trees ($r^2=0.78$, $f_{2,54} = 199.6$, $p = 0.0001$ and $r^2 = 0.81$, $f_{2,13} = 55.9$, $P = 0.0001$ respectively). However, the slope of the line describing the relationship between T_a and T_r for *Banksia* roosts was significantly greater than that for roosts in *Melaleuca* trees (test of slopes: $t_{67} = 5.6$, $P < 0.001$) and at T_a s above about 16°C the temperatures in *Banksia* roosts was always greater than those in *Melaleuca*. In addition, in *Banksia* trees T_r typically approached T_a by about 1200 and by the time final temperature measurements were taken (between 1600 and 1700) five of six roosts in *Banksia* had temperatures that exceeded ambient by about 1.0°C (range $0.3\text{--}1.7^\circ\text{C}$; Fig 3). The temperature of roosts in *Melaleuca* trees never exceeded T_a during the measurement periods (Fig 3).

Discussion

Nyctophilus geoffroyi roost in trees and change roost regularly. This habit has been recorded in a number of other Australian forest bats (L Lumsden, *pers. comm.*; Lunney *et al.* 1988, 1995) and is consistent with the proposal that roost fidelity is directly related to roost permanence (Lewis 1995). The same may also be true of *N. major*.

In a study of roost use by bats in Tasmania, Taylor &

Savva (1988) noted that *N. geoffroyi* change roosts frequently. They located two roosts under bark, one in a narrow cavity in a tree bole, and one in a fissure. However, unlike this study, *N. geoffroyi* were only found roosting in a dead tree once. In remnant vegetation around farmland in Victoria, *N. geoffroyi* were found to roost disproportionately in dead trees, a finding similar to that reported here (L Lumsden, *pers. comm.*).

The preference that *N. geoffroyi* displayed for dead *Banksia* trees over live *Melaleuca* trees, during this study, probably relates to different winter thermal characteristics of roosts found in the two tree species. By choosing *Banksia* roosts, *N. geoffroyi* are exposed to temperatures above ambient during the late afternoon and this would reduce the costs of arousal from torpor prior to foraging. It was noted that many roosts in *Banksia* trees were facing the afternoon sun and this may explain why T_r was higher than T_a in the afternoon in *Banksia* tree roosts. In addition, dead *Banksia* trees were dark coloured, which presumably aids heating further. If the same thermal characteristics are found during summer, it is reasonable to expect *Melaleuca* trees to be the preferred roost. With their apparently superior insulation, *Melaleuca* would be cooler than *Banksia* roosts; low temperatures enable bats to lower their body temperature, leading to water and energy savings (*e.g.* Hosken & Withers *in press*). That *N. major* were found to

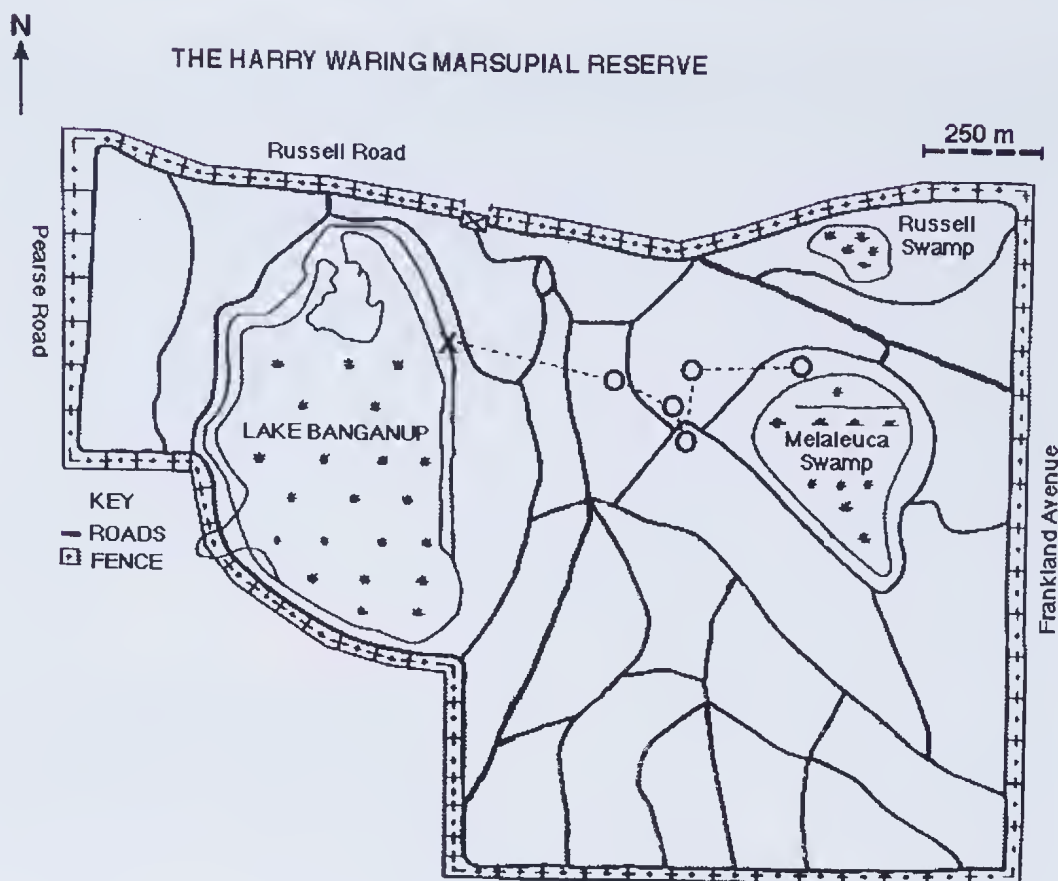


Figure 2. Map of the Harry Waring Marsupial Reserve showing the roost movement patterns of a female *N. geoffroyi*. x = site of capture, o = roost locations, dotted lines show bat movement between roosts.

frequently use these trees during summer appears to support this reasoning, but further investigation is required. No bats were found roosting in live *Banksia* trees. This is probably due to the fact that the bark is not loose on live trees and further indicates that *N. geoffroyi* are selecting specific roost sites.

The use of *Melaleuca* roosts during rainy periods probably relates to the fact that these trees are not water harvesting, and roosts under the multilayered bark insulation stay dry, while roosts in dead *Banksia* trees were often damp during and after rain. In addition, storms appear to exact a heavier toll on dead *Banksia* trees when compared with *Melaleuca* trees; four dead *Banksia* trees were found across tracks after storms during the course of the study. This also indicates that the *Banksia* roosts are relatively ephemeral, which makes the reliance on one roost unprofitable and possibly prompts frequent roost movement. All trees that were found to contain roosts during this study were tagged and longer term observation will reveal the longevity of each roost.

In this study, *N. geoffroyi* were found to roost alone. This is consistent with other published reports (Lumsden & Bennett 1995, Taylor & Savva 1988). However, Taylor & Savva (1988) also found three colonies containing three, 12 and 23 *N. geoffroyi*. The two largest groups were maternity colonies. Since this study was carried out during autumn and winter, no maternity colonies were

encountered and it appears that these bats, at least in *Banksia* woodland, are solitary during the mating period which extends from about April to September (Hosken, unpublished data).

As with *N. gouldi* (Lunney *et al.* 1988), *N. geoffroyi* appear to display fidelity to an area and the distances between successive roosts reported here are similar to those reported for other nyctophilines (Lunney *et al.* 1988, 1995). The largest distance between capture site and roost site for *N. geoffroyi* in this study was about 1200m. This is similar to the distances moved by male *N. geoffroyi* in Victoria (L Lumsden *pers. comm.*) but less than the 4800m reported by Taylor and Savva (1988) and the 6–12km reported for female *N. geoffroyi* (L Lumsden *pers. comm.*). However, the comparatively small distances between capture site and roost site reported here are consistent with the flight morphology of *N. geoffroyi* which indicates that this species is not suited to long distance flight (Fullard *et al.* 1991). A similar finding is reported here for *N. major*. The only individual which regularly changed roosts during this study was found to move about the same distance as the *N. geoffroyi*. This *N. major* shed its transmitter at its initial capture site five days after capture. This was approximately 1200m from its last roost tree. *N. major* is reported to have flight characteristics similar to *N. geoffroyi* (Hall & Richards 1979), which suggests that long distance flight would also be energetically expensive for this species.

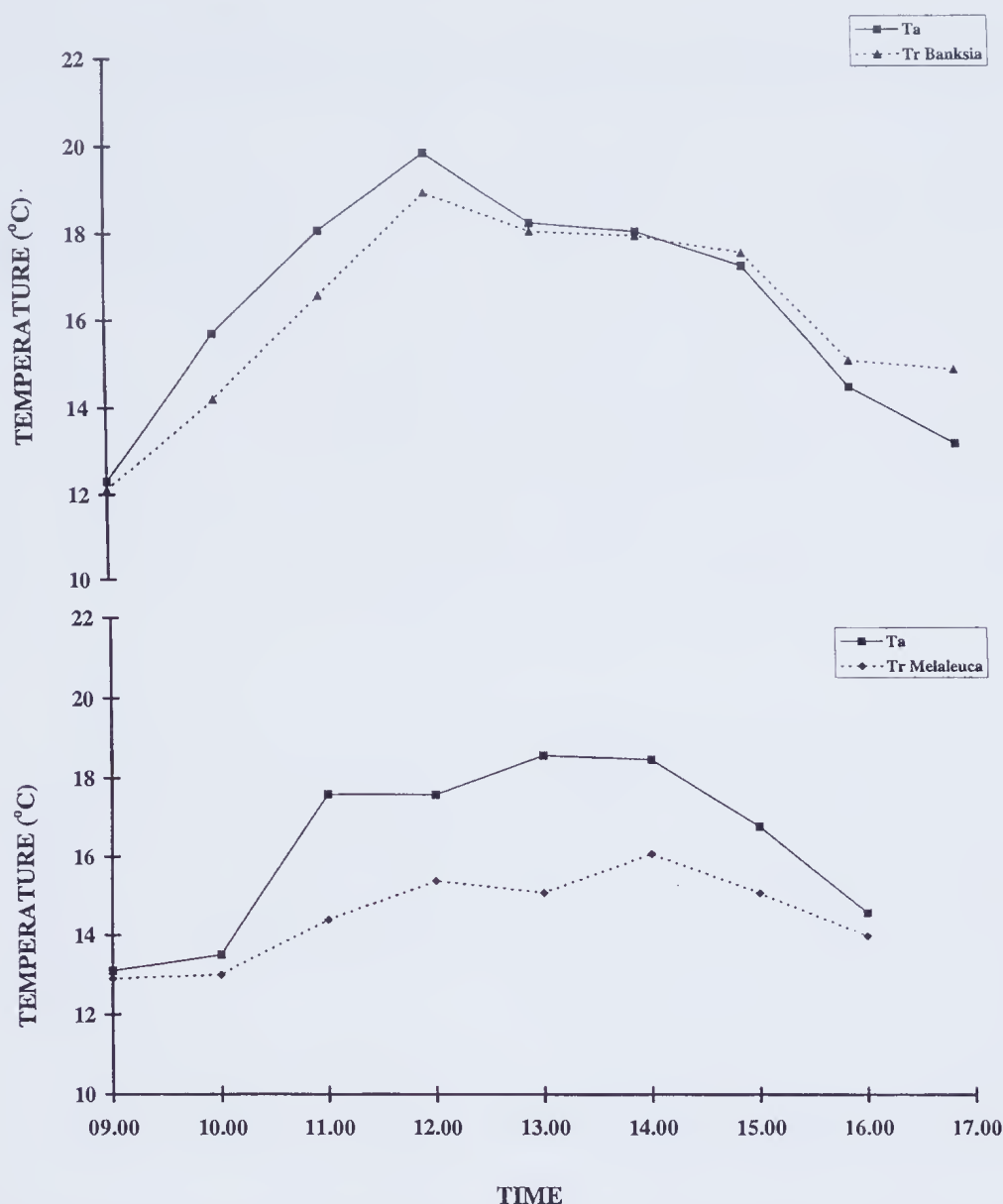


Figure 3. Hourly changes in the roost temperature of a typical *Banksia* roost (top) and a typical *Melaleuca* roost (bottom) plotted with T_a measured outside but adjacent to the roost.

The use of only large mature or dead trees by both the bat species tracked during this study indicates that a mature forest is essential for them. The finding that dead trees were the predominant roost used by *N. geoffroyi* and that these trees appear to be the main victims of winter storm indicates that the continual tree death is required to maintain the roosts needed by these small bats. Unfortunately, continued clearing on the Swan Coastal Plain may eventually threaten this continuity.

Acknowledgments: I am grateful to numerous people who helped at various stages of this study, particularly A F Stucki and B Cooper. My thanks are extended to N McKenzie (Department of Conservation and Land Management, Perth, WA), H Parnaby (The Australian Museum, Sydney, NSW) and L Lumsden (Department of Conservation and Natural Resources, Heidelberg, VIC) for advice, comments and access to unpublished information. I also thank A Thompson, P C Withers, J E O'Shea and two anonymous referees who commented on earlier drafts of this paper. Bats were captured under permit numbers BB685 and SF1700 issued by the Department of Conservation and Land Management.

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Waterbirds and aquatic invertebrates of swamps on the Victoria-Bonaparte mudflat, northern Western Australia

S A Halse¹, R J Shiel² & G B Pearson¹

¹Department of Conservation and Land Management, Wildlife Research Centre, PO Box 51 Wanneroo, WA 6065

²Murray-Darling Freshwater Research Centre, PO Box 921 Albury, NSW 2640

Manuscript received May 1996; accepted October 1996

Abstract

The aquatic invertebrate and waterbird faunas of the western part of the Victoria-Bonaparte mudflat, located in the Victoria-Bonaparte biogeographic region of the Kimberley, Western Australia, were surveyed in early 1993. Sixty-two species of waterbird and at least 131 species of aquatic invertebrate were recorded. The mudflat has national significance for some shorebird species, especially Redshanks, and has a significant Asian element in the invertebrate fauna. The survey contributes to growing evidence that the micro-invertebrate fauna of Western Australia is distinctive, but the conservation significance of the area for invertebrates cannot be assessed properly without more information concerning other areas of northern Australia.

Introduction

Australia has been divided into 80 biogeographic regions, based on climate, geology, landform, flora, fauna and land use, to provide a framework for assessing the adequacy of Australia's system of conservation reserves (Thackway & Cresswell 1995). The Victoria-Bonaparte mudflat, an extensive area that is occasionally inundated by fresh or saline water, is within the Victoria-Bonaparte biogeographic region in the extreme north-eastern Kimberley area of Western Australia.

Approximately 1,000,000 palaearctic shorebirds occur annually in coastal habitats of northern Australia, with major concentrations at Eighty-Mile Beach and Roebuck Bay, in Western Australia, and the Gulf of Carpentaria, in Queensland (Lane 1987). These areas are staging points for shorebirds as they migrate to and from Australia. Many shorebirds remain in northern Australia over the austral winter, rather than returning to the Northern Hemisphere to breed, but Minton & Martindale (1982) recorded only 7120 shorebirds along the coast between Darwin and Kununurra, including the Victoria-Bonaparte mudflat, during an aerial survey in late August 1981. As a result, subsequent shorebird studies in north-western Australia have been concentrated further south in the Kimberley and in the Pilbara, where more shorebirds had been recorded (*e.g.* Minton & Jessop 1994).

Most information about aquatic invertebrates in lentic waters of northern Australia comes from studies in the Alligator Rivers region of the Northern Territory (*e.g.* Tait *et al.* 1984; Julli 1986; Hawking 1992) and extensive collecting by B V Timms (Timms 1988; Timms & Morton 1988). Information for the Kimberley is virtually restricted to the work of Timms, and what can be extracted from taxonomic and biogeographic papers that are mostly based on the collections of Williams (1979) and Timms (*e.g.* McKenzie 1966; Watts 1987). Recent work

has shown that the stream fauna of the Kimberley is comparatively rich (M J Smith, W R Kay & S A Halse, unpublished observations) in contrast to the tentative suggestion of Williams (1979) that it was depauperate. The only comprehensively studied lentic site in the Kimberley, Lake Gregory on the edge of the Great Sandy Desert, also supported a rich fauna (Halse *et al.* in press). McKenzie (1966) commented on the apparent affinities of the ostracod faunas of the Kimberley and Indonesian islands. Lansbury (1984) suggested that the hemipteran fauna of coastal Kimberley waterbodies has similar Indonesian links, unlike the remainder of Australia.

The biology of the Victoria-Bonaparte biogeographic region, like much of the Kimberley area, is poorly known, and less than 10 per cent of the Western Australian portion is reserved. In a review of the conservation reserve system of the Kimberley, Burbidge *et al.* (1991) recommended that the conservation value of the Victoria-Bonaparte mudflat be investigated, and McKenzie *et al.* (1991) examined two rainforest patches (EK05, EK06). The aim of the present study was to gather information on waterbirds and aquatic invertebrates using the mudflat. The conservation value of the mudflat and the biogeographic affinities of some invertebrate taxa are discussed.

Study area

The Victoria-Bonaparte mudflat is a band approximately 10-20 km wide along the coast of Joseph Bonaparte Gulf, between Cambridge Gulf in Western Australia and the mouth of the Victoria River in the Northern Territory (Fig 1). Tidal flats up to 2 km wide and a narrow sandy beach occur on the northern side of the mudflat, south of which is an elevated narrow band of low dunes between the beach and a hinterland of extensive bare mudflat. Several creeks, lined by mangroves, drain the mudflat. Along the landward boundary there are many small freshwater pools and some larger areas of freshwater marsh.

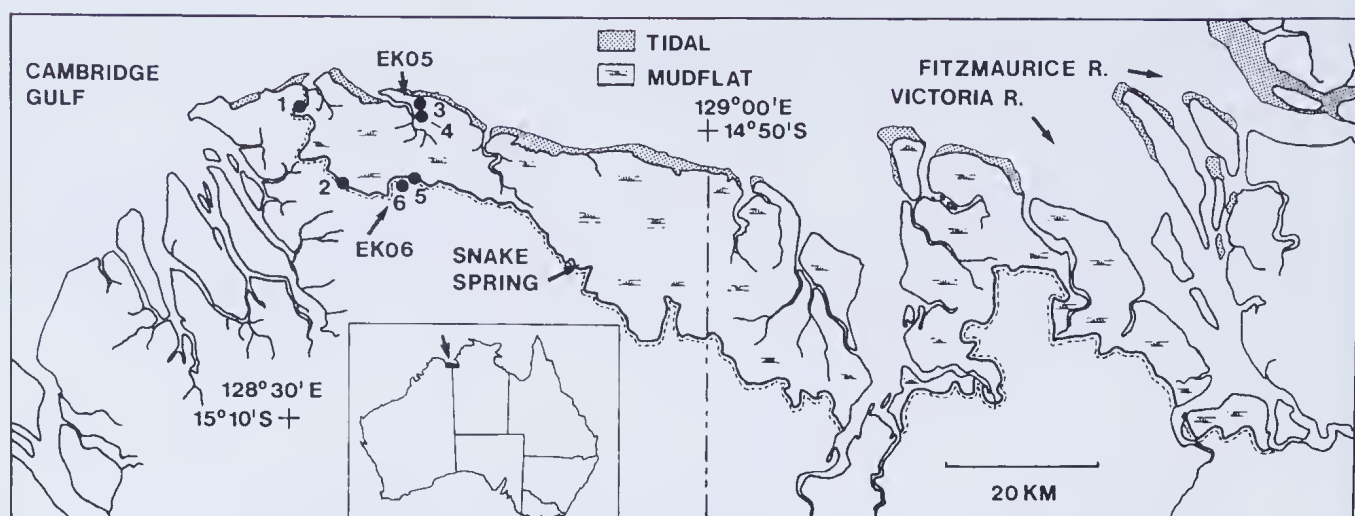


Figure 1. Victoria-Bonaparte mudflat, showing the sampling sites for aquatic invertebrates and other features mentioned in text (the boundary of the mudflat in the Northern Territory is drawn approximately). 1, Grassed Pool; 2, Brolga Spring; 3, Samphire Pool; 4, Mudflat Pool; 5, Rainforest Swamp; 6, Edge Swamp

Several shallow, seasonally inundated freshwater pools covered with emergent grass *Vetiveria pauciflora* and sedges *Cyperus conicus* and *C. javanicus* occur at the north-western end of the mudflat (Fig 1). The northernmost of the pools is referred to as Grassed Pool. At the south-western end is a small permanent swamp, Brolga Spring, which contains *Melaleuca viridiflora* trees and *Sesbania cannabina* on the southern side. There are two shallow pools east of the mouth of the second largest creek on the mudflat, near the coastal rainforest site, EK05 (McKenzie *et al.* 1991). The freshwater, seasonal Samphire Pool is located in an interdunal swale and supports emergent samphire *Halosarcia halocnemoides tenuis* and sedge *Cyperus aquatilis*, while the brackish, tidally filled Mudflat Pool lies in a depression on the southern side of the dune area with a shallow drainage line connecting it to bare mudflat; it has some emergent grass. Rainforest Swamp, a small semi-permanent freshwater swamp, containing tall *Melaleuca argentea* and *Nauclea orientalis* trees and small herbaceous ferns such as *Cyclosorus interruptus* and *Blechnum orientale*, was adjacent to the rainforest site, EK06, near Long Spring (McKenzie *et al.* 1991). There is also a small seasonal freshwater swamp at Long Spring between the fringing woodland and open mudflat, referred to herein as Edge Swamp. Around Snake Spring, on the southern edge of the central part of the mudflat, extensive areas are ephemerally flooded with fresh water via small creeks from the south and covered with dense stands of grass and sedge.

Methods

Waterbirds were counted from 17-19 February by SAH and from 4-6 April by SAH and GBP in 1993 to document the numbers and species of waterbirds using the area in late summer, during the middle of the wet season, and in autumn when migratory shorebirds are concentrated in northern Australia prior to leaving for the Northern Hemisphere. A partial count of the Western Australian

portion of the Victoria-Bonaparte mudflat was made from a Cessna 182 flying at a height of 30-40 m and speed of 100 knots on 17 February. On 18-19 February, several marine and freshwater sections of the mudflat were counted from a Robinson helicopter flying at a height of 15 m and speed of 50 knots. In addition, ground counts were made at Snake Spring, Grassed Pool and on 4 km of tidal flat north of EK05. On 4 April, ground counts were made among mangroves and on tidal flat west of the creek mouth at EK05, and at the second-most north-western grassed pool (Fig 1). On 5-6 April, a complete count of the Western Australian portion of the mudflat was made from a Cessna 182 flying at a height of 20 m and speed of 60 knots.

Two samples of aquatic invertebrates were collected from Grassed Pool, Samphire Pool, Mudflat Pool, Rainforest Swamp and Edge Swamp by SAH on 18-19 February by sweeping approximately 50 m of water, and as many microhabitats as possible, using FBA-type pondnets with 50 and 110 μ m mesh. The 50 μ m mesh sample was preserved in 5 per cent buffered formalin, the 110 μ m mesh sample was preserved in 70 per cent alcohol for sorting and identification in the laboratory. Water samples were taken from four of the sites for measurement of conductivity (mS cm^{-1} ; TPS LC81), which was converted to parts per thousand total dissolved solids (ppt TDS) as $\text{TDS} = 0.6 \text{ mS cm}^{-1}$.

Results

Altogether, 62 species of waterbird were recorded on the Western Australian portion of the Victoria-Bonaparte mudflat, including 28 species of shorebird (Table 1). More than 4,000 birds were counted in both February and April, with almost 2000 shorebirds present each occasion. Notable records in February were 1701 Magpie Geese, mostly near Snake Spring, 126 Marsh Sandpipers near Snake Spring and Grassed Pool, and 5 Redshanks on the creek near EK05. Notable records in April were

Table 1

Waterbirds recorded on the Victoria-Bonaparte mudflat in February and April 1993

Species	Feb	April
Magpie Goose <i>Anseranas semipalmata</i>	1701	10
Plumed Whistling-Duck <i>Dendrocygna eytoni</i>	20	6
Wandering Whistling-Duck <i>Dendrocygna arcuata</i>	12	
Radjah Shelduck <i>Tadorna radjah</i>	11	5
Green Pigmy-Goose <i>Nettapus pulchellus</i>	11	1
Pacific Black Duck <i>Anas superciliosa</i>	39	37
Grey Teal <i>Anas gracilis</i>	32	
Hardhead <i>Aythya australis</i>	1	
Darter <i>Anhinga melanogaster</i>	3	
Little Pied Cormorant <i>Phalacrocorax melanoleucus</i>	30	
Little Black Cormorant <i>Phalacrocorax sulcirostris</i>	11	
Australian Pelican <i>Pelecanus conspicillatus</i>	23	17
Little Egret <i>Egretta garzetta</i>	42	54
Eastern Reef Egret <i>Egretta sacra</i>	6	1
Pied Heron <i>Ardea pictata</i>		4
Great Egret <i>Egretta alba</i>	5	6
Intermediate Egret <i>Egretta intermedia</i>	2	2
Unidentified egret	48	99
Striated Heron <i>Butorides striatus</i>		2
Nankeen Night Heron <i>Nycticorax caledonicus</i>	18	1
Glossy Ibis <i>Plegadis falcinellus</i>		59
Australian White Ibis <i>Threskionis aethiopica</i>	183	281
Straw-necked Ibis <i>Threskionis spinicollis</i>		30
Black-necked Stork <i>Xenorhynchus asiaticus</i>	14	6
Sarus Crane <i>Grus antigone</i>		2
Brolga <i>Grus rubicundis</i>	18	81
Black-tailed Godwit <i>Limosa limosa</i>	2	2
Bar-tailed Godwit <i>Limosa lapponica</i>	30	171
Whimbrel <i>Numenius phaeopus</i>	21	53
Eastern Curlew <i>Numenius madagascariensis</i>	6	5
Little Curlew <i>Numenius minutus</i>		1
Common Redshank <i>Tringa totanus</i>	5	
Marsh Sandpiper <i>Tringa stagnatilis</i>	126	83
Common Greenshank <i>Tringa nebularia</i>	13	65
Wood Sandpiper <i>Tringa glareola</i>		3
Terek Sandpiper <i>Tringa terek</i>		29
Common Sandpiper <i>Tringa hypoleucos</i>		1
Grey-tailed Tattler <i>Tringa brevipes</i>		15
Ruddy Turnstone <i>Arenaria interpres</i>		5
Great Knot <i>Calidris tenuirostris</i>	10	74
Red Knot <i>Calidris canutus</i>	5	
Red-necked Stint <i>Calidris ruficollis</i>		34
Sharp-tailed Sandpiper <i>Calidris acuminata</i>	1	
Curlew Sandpiper <i>Calidris ferruginea</i>	2	2
Comb-crested Jacana <i>Irediparra gallinacea</i>	2	
Beach Stone-Curlew <i>Burhinus neglectus</i>	2	1
Pied Oystercatcher <i>Haematopus longirostris</i>	36	21
Black-winged Stilt <i>Himantopus himantopus</i>	101	261
Red-necked Avocet <i>Recurvirostra novaehollandiae</i>	1	
Pacific Golden Plover <i>Pluvialis dominica</i>	1	1
Grey Plover <i>Pluvialis squatarola</i>	1	14
Red-capped Plover <i>Charadrius ruficapillus</i>	11	2
Greater Sand Plover <i>Charadrius leschenaultii</i>	3	43
Red-kneed Dotterel <i>Erythronyx cinctus</i>		1
Masked Lapwing <i>Vanellus miles</i>	37	120
Unidentified wader	1559	903
Silver Gull <i>Larus novaehollandiae</i>	5	3
Gull-billed Tern <i>Gelochelidon nilotica</i>	7	133
Caspian Tern <i>Hydroprogne caspia</i>	3	6
Crested Tern <i>Sterna bergii</i>	1	
Little Tern <i>Sterna albifrons</i>	1	32
Whiskered Tern <i>Chlidonias hydrida</i>		37
White-winged Black Tern <i>Chlidonias leucoptera</i>		1123
Unidentified tern	162	354
Clamorous Reed-Warbler <i>Acrocephalus stentoreus</i>		2
Total	4384	4304

1123 White-winged Black Terns and 53 Whimbrels. Counts for some species, especially shorebirds and terns, were under-estimates because not all birds could not be identified to species level during the aerial surveys and categories such as 'unidentified tern' were used. Estimates of total waterbird numbers were probably reasonably accurate, however (see Halse *et al.* 1996).

All sites sampled for invertebrates on the Victoria-Bonaparte mudflat, except Mudflat Pool (11.8 ppt TDS), were fresh. The salinity of Samphire Pool was 0.84 ppt, Brolga Spring was 0.51 ppt and Edge Swamp was 0.20 ppt. At least 131 species of invertebrate were collected, with the number of species per site ranging from 13 at the brackish Mudflat Pool to 60 at Edge Swamp (Appendix). Species-rich orders were Cladocera (27 species), Ploimida (24), Coleoptera (20), Copepoda (10) and Ostracoda (10).

A significant number of species were undescribed. Apart from *Metacyclops* sp. EK1, these included the ostracods *Bennelongia* sp. 363, *Cyprinotus* sp. 362 and *Ilyodromus* sp. 365, cladocerans *Macrothrix* sp. A and *Macrothrix* sp. B and rotifers *Lecane* sp. A and *Lecane* sp. B (Appendix). The ostracod, *Straudesia/Chamydotheca* sp., appeared to be an undescribed genus (P De Deckker, pers. comm.). Many of the insect larvae, especially dipterans, could not be identified to species because the taxonomy of the larvae is poorly known.

Discussion

Fewer waterbird species (62) occurred on the Western Australian portion of the Victoria Bonaparte mudflat during the two surveys than have been recorded on the long-term list for Parry Lagoons (77), which is the best known site for waterbirds in the Victoria-Bonaparte biogeographic region (Jaensch & Lane 1993). Total numbers were substantially lower than the highest counts at Parry Lagoons and 4304 birds of 50 species were recorded on the mudflat in April, compared with 8145 birds of 33 species at Parry Lagoons on the same day (aerial survey, S A Halse & G B Pearson, unpublished observations). Nevertheless, the mudflat is more important for waterbirds, especially shorebirds, than previously thought. Because of the greater range of habitat for shorebirds, especially tidal flats, the two surveys of the mudflat yielded 28 species of shorebird compared with the long-term list of 24 for Parry Lagoons.

In April, 1910 shorebirds were counted on the Western Australian portion of the Victoria-Bonaparte mudflat, with a further 6642 counted between the Northern Territory border and the Fitzmaurice River, an overall distance of approximately 250 km (Fig 1). In February, 1973 shorebirds were counted on the mudflat. These counts represent higher densities than observed by Minton & Martindale (1982), who recorded 7120 shorebirds on the 630 km between Darwin and Kununurra. The mudflat also has national significance for several shorebird species (see Watkins 1993). The 5 Redshanks seen in February comprised as large a flock as has been recorded in Australia, equalled only by 5 birds at Broome in April 1985 (Lane & Jessop 1985; Hewish 1987). It is possible that other Redshanks were present on the creek near EK05, or on other parts of the mudflat. Australian

records are mostly restricted to north-western Australia and the Victoria-Bonaparte mudflat must be regarded as one of the more important Australian sites for the species. Although the count of 53 Whimbrels at the mouth of the creek near EK05 in April under-estimated the number on the whole mudflat, when combined with 235 Whimbrels seen on the same day in the Northern Territory between the Fitzmaurice River and Western Australian border (S A Halse & G B Pearson, unpublished observations), the total count for the 250 km length of coast was the seventh highest for the species in Australia (Watkins 1993). The count of 126 Marsh Sandpipers in February, although an under-estimate of the number on the whole mudflat, was the fifteenth highest count in Australia (Watkins 1993).

The conservation value of the Victoria-Bonaparte mudflat for aquatic invertebrates is difficult to evaluate because there have been few studies in similar areas. The floodplains of the Alligator Rivers region appear to support more species; Shiel & Koste (1983) recorded an average of 34 rotifer species per sample and Julli (1986) recorded approximately 20-30 species of cladocerans compared with 2-15 rotifers and 2-13 cladocerans at sites on the mudflat. On the other hand, with 28-60 species at freshwater sites the mudflat compared well with Lake Gregory, in the southern Kimberley which, when fresh, averaged 35 species per site (Halse *et al.* in press; S A Halse, unpublished observations).

The distributions of most species of aquatic invertebrates in northern Australia are poorly known and, therefore, the significance of unusual records on the mudflat is difficult to assess. For example, the only previous record of the harpacticoid copepod *Cletocamptus confluens* in Australia was from Peron Peninsula, Shark Bay, 2000 km south-west of the mudflat (Lang 1948), so its occurrence at Mudflat Pool has conservation implications, except there have been so few invertebrate surveys that the species may well be widespread. Likewise, at present many aquatic habitats in the Kimberley support significant numbers of undescribed species and this, by itself, cannot be used as evidence of special conservation value. A recent study of land snails in rainforest patches of the Kimberley found that at least 36 per cent, and perhaps as many as 50 per cent, of species collected were undescribed (Solem 1991). All 26 pseudoscorpion species collected in the same study were undescribed (Harvey 1991), as were the 11 indigenous earthworm species (McKenzie & Dyne 1991).

It is worth noting that, in addition to obviously undescribed taxa, several taxa collected on the mudflat differed only slightly from descriptions of known species. Without collections from other localities and detailed analyses, it is impossible to determine whether the small differences represented geographic variation or new species. We have listed these taxa as having affinity to known species, including the rotifer *Scaridium elegans* and the cladoceran *Moina weismanni*, both of which have not been recorded in Australia previously.

The rotifers of northern Australia have strong Indo-Malaysian affinities (Shiel & Williams 1990) and this seems to be the case for much of the crustacean fauna on the Victoria-Bonaparte mudflat. The cladoceran fauna of northern Australia has a strong circumtropical element

(Timms 1988) and several genera with Indo-Malaysian affinities, such as *Pseudosida*, *Grimaldina* and *Moinadaphnia*, occurred on the mudflat. The undescribed cyclopoid copepod, *Metacyclops* sp EK1, is unlike other Australian *Metacyclops* and has affinities with species from north of Australia (D W Morton, personal communication). Similarly the ostracod, *Cypris subglogosa*, which was recorded in Australia for the first time, is widespread in ricefields of equatorial regions, Asia and eastern Europe (Okubo 1972a). *Cyprinotus kimberleyensis*, which appears to be widespread in the Kimberley, is also found in Asian ricefields (Okubo 1974) and the ostracod genus, *Strandesia*, which was well represented in the mudflat samples, is common throughout Asia (e.g. Okubo 1972b; Victor *et al.* 1980).

In conclusion, the Victoria-Bonaparte mudflat is a nationally significant area for waterbirds, especially shorebirds, although the numbers of birds found there is not as high as in some other areas of the Kimberley. The use of the area by Redshanks, a species that mostly stops in southern Asia during the austral summer, is consistent with the occurrence of invertebrates on the mudflat that have Asian affinities. A more comprehensive inventory of invertebrate species and their distributions is required before the relative significance of the Victoria-Bonaparte mudflat for the conservation of invertebrates can be assessed. However, the survey supported Lansbury's (1984) suggestion that there is a strong Asian element in the invertebrate fauna of the coastal Kimberley and added to the growing evidence that Western Australia has a distinctive micro-invertebrate fauna (Frey 1991; Maly & Bayly 1991; Storey *et al.* 1993).

Acknowledgments: We thank G J Keighery for floristic information and A Clarke for sorting the invertebrate samples. P De Deckker (ostracods), R Hamond (harpacticoids), M S Harvey (water mites), J Hawking (odonates), W R Kay and I Lansbury (hemipterans), D W Morton (cyclopoids), S Slack-Smith (gastropods), M J Smith (chironomids) and C H S Watts (beetles) assisted with identifications. The February sampling trip was funded by the Department of Environment, Sport and Territories, and the March trip was partly funded by the Australian Nature Conservation Agency under the States Cooperative Assistance Program.

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Appendix

Taxa of aquatic invertebrates collected at six sites on the Victoria-Bonaparte mudflat in February 1993. 1, present; 1a, adult beetles; 1b, larval beetles only

Taxon	Mudflat Pool	Samphire Pool	Edge Swamp	Rainforest Swamp	Grassed Pool	Brolga Spring
PROTISTA						
LOBOSEA						
ARCELLINIDA						
Arcellidae						
<i>Centropyxis aculeata</i> (Ehrenberg)					1	
ROTIFERA						
DIGONONTA						
BDELLOIDEA						
Bdelloidea sp.		1				1
MONOGONONTA						
FLOSCULARIACEA						
Hexarthridae						
<i>Hexarthra intermedia</i> Wiszniewski			1			
Filinidae						
<i>Filinia longiseta</i> (Ehrenburg)			1			1
Testudinellidae						
<i>Testudinella patina</i> (Hermann)			1		1	1
PLOIMIDA						
Asplanchnidae						
<i>Asplanchna brightwelli</i> (Gosse)			1			
Brachionidae						
<i>Anuraeopsis fissa</i> (Gosse)			1	1		
<i>Brachionus angularis</i> Gosse						1
<i>Brachionus quadridentatus</i> Hermann			1			1
<i>Brachionus</i> sp. C			1			
<i>Platyias quadricornis</i> Ehrenberg			1	1		1
Notomammatidae						
<i>Cephalodella</i> sp.					1	
<i>Scaridium</i> aff. <i>elegans</i> Segers & De Meester			1			
Synchaetidae						
<i>Polyarthra dolichoptera</i> Nelson			1			
Lecanidae						
<i>Lecane</i> (<i>Monostyla</i>) <i>bulli</i> Gosse				1	1	1
<i>Lecane</i> (<i>Monostyla</i>) <i>hamata</i> Stokes			1			
<i>Lecane</i> (s. str.) <i>curvicornis</i> (Murray)			1	1		
<i>Lecane</i> (s. str.) <i>luna</i> (Muller)		1	1		1	1
<i>Lecane</i> (s. str.) <i>leontina</i> (Turner)			1		1	1
<i>Lecane</i> (s. str.) <i>ludwigi</i> (Eckstein)						1
<i>Lecane</i> (s. str.) <i>ungulata</i> (Gosse)			1		1	
<i>Lecane</i> (s. str.) sp. nov. A					1	
<i>Lecane</i> (s. str.) sp. nov. B				1		
<i>Lecane</i> (s. str.) sp.	1					
Euchlanidae						
<i>Dipleuchlanis propatula</i> (Hudson & Gosse)					1	
<i>Dipleuchlanis</i> sp. B			1			
<i>Euchlanis dilatata</i> Ehrenberg			1			
<i>Euchlanis</i> sp. B			1		1	1
Mytilinidae						
<i>Mytilina acanthophora</i> Hauer				1		
Trichotriidae						
<i>Trichotria</i> sp.			1			
MOLLUSCA						
GASTROPODA						
BASOMMATOPHORA						
Planorbidae						
<i>Physastra</i> sp.				1		
<i>Gyraulus</i> sp.				1		
Lymnaeidae						
<i>Lymnaea</i> sp.				1		
ARTHROPODA						
ARACHNIDA						
HYDRACARINA						
Pionidae						
<i>Piona australica</i> K O Viets					1	
Hydrachnidae						
<i>Hydrachna</i> sp.						1
CRUSTACEA						
NOTOSTRACA						
Triopsidae						
<i>Triops australiensis</i> Spencer & Hall					1	
CLADOCERA						
Sididae						

Taxon	Mudflat Pool	Samphire Pool	Edge Swamp	Rainforest Swamp	Grassed Pool	Brolga Spring
<i>Diaphanosoma</i> aff. <i>unguiculatum</i> Gurney			1	1	1	1
<i>Latonopsis</i> sp.						1
<i>Pseudosida szalaii</i> Daday			1			
<i>Sarsilatona papuana</i> (Daday)			1	1		
Chydoridae						
<i>Alona</i> aff. <i>rectangula</i> Sars					1	
<i>Alona rectangula novaezealandiae</i> (Sars)				1	1	
<i>Alona</i> aff. <i>setuloides</i> Smirnov & Timms					1	
<i>Alona</i> aff. <i>costata</i> Sars		1	1		1	
<i>Alona</i> sp. A			1			
<i>Alona</i> ? sp. nov. B					1	
<i>Biapertura</i> aff. <i>karua</i> (King)			1			1
<i>Biapertura</i> aff. <i>setigera</i> (Brehm)			1			
<i>Dunhevedia crassa</i> King			1			1
<i>Kurzia longirostris</i> (Daday)				1		
<i>Ledydia acanthocercoides</i> (Fischer)					1	
<i>Ledydia</i> aff. <i>ciliata</i> Gauthier			1		1	
Macrothricidae						
<i>Grimaldina brazzaei</i> Richard				1		
<i>Macrothrix</i> aff. <i>capensis</i> (Sars)					1	
<i>Macrothrix</i> aff. <i>timmsi</i> Smirnov					1	
<i>Macrothrix triserialis</i> Brady				1		
<i>Macrothrix</i> sp. nov. A			1	1		
<i>Macrothrix</i> sp. nov. B			1	1		
Moinidae						
<i>Moinadaphnia macleayi</i> (King)				1		
<i>Moina</i> aff. <i>micrura</i> Kurz			1		1	
<i>Moina</i> aff. <i>weismanni</i> Ishikawa		1	1		1	1
Daphniidae						
<i>Ceriodaphnia</i> sp.						1
<i>Simocephalus</i> sp.						1
OSTRACODA						
Ilyocyprididae						
<i>Ilyocypris australiensis</i> Sars			1			
<i>Beninelongia</i> sp. 363					1	
<i>Cyprinotus</i> sp. 362					1	
<i>Cypretta baylyi</i> McKenzie			1	1		
<i>Cyprinotus kimberleyensis</i> McKenzie	1	1	1	1	1	1
<i>Cypris subglobosa</i> Sowerby			1			
<i>Ilyodromus</i> sp. 365			1			
<i>Strandesia</i> ? <i>camaguinensis</i> Tressler				1		1
<i>Strandesia</i> sp. 360				1		
<i>Strandesia/Chlamydotheca</i> gen nov. 357				1		
CONCHOSTRACA						
Cyzicidae						
<i>Cyzicus</i> sp. A					1	
<i>Cyzicus</i> sp. B		1				
Cyclestheriidae						
<i>Cyclestheria</i> sp.					1	
COPEPODA						
Centropagidae						
<i>Diaptomus</i> sp.				1		
Cyclopoidae						
<i>Apocyclops dengizicus</i> (Lepeschkin)	1	1				
<i>Mesocyclops</i> ? <i>australiensis</i> (Sars)					1	1
<i>Mesocyclops</i> sp. LS2				1		1
<i>Metacyclops</i> sp. EK1	1	1				
<i>Microcyclops varicans</i> (Sars)			1	1	1	
<i>Thermocyclops</i> sp. LS1			1	1		
Canthocamptidae						
<i>Cletocamptus confluens</i> Kiefer	1					
<i>Cletocamptus dietersi</i> (Richard)		1				
<i>Canthocamptidae</i> sp. 267				1		
DECAPODA						
Hymenosomatidae						
<i>Holthuisiana transversa</i> (von Martens)				1		
INSECTA						
EPHEMEROPTERA						
Baetidae						
<i>Clocon</i> sp.		1		1		1
ZYGOPTERA						
Coenagrionidae						
<i>Coenagrionidae</i> sp.						1
ANISOPTERA						
<i>Anisoptera</i> sp.		1	1		1	
Aeschnidae						
<i>Hemianax papuensis</i> (Burmeister)				1		

Taxon	Mudflat Pool	Samphire Pool	Edge Swamp	Rainforest Swamp	Grassed Pool	Brolga Spring
Gomphidae						
<i>Hemigomphus</i> sp.		1				
Libellulidae						
<i>Diplacodes bipunctata</i> (Brauer)	1	1				
<i>Pantala flavescens</i> (Fabricius)	1	1				
HEMIPTERA						
Gerridae						
? <i>Limmogonus</i> sp.				1		
Corixidae						
<i>Micronecta</i> aff. <i>virgata</i> Hale		1	1			1
Nepidae						
<i>Austronepea angustata</i> (Hale)				1		
Belostomatidae						
<i>Lethocerus</i> sp.			1			
Notonectidae						
<i>Anisops malkini</i> Brooks		1				1
<i>Anisops nasuta</i> Fieber	1	1			1	1
<i>Anisops</i> sp.			1			
DIPTERA						
Culicidae						
<i>Culex annulirostris</i> Skuse		1	1	1	1	1
Chironomidae						
<i>Chironomus</i> sp.	1	1	1		1	1
<i>Cladotanytarsus</i> sp. K4						1
<i>Larsia albiceps</i> (Johannsen)						1
<i>Procladius paludicola</i> (Skuse)			1			1
<i>Tanytarsus</i> aff. K12					1	
Stratiomyidae						
Stratiomyidae sp.		1	1			
Ephydriidae						
Ephydriidae sp.						1
Tabanidae						
Tabanidae sp.	1					
LEPIDOPTERA						
Pyalidae						
Pyalidae sp. 1			1		1	
Pyalidae sp. 2			1			
TRICHOPTERA						
Leptoceridae						
Leptoceridae sp.			1			
COLEOPTERA						
Gyrinidae						
<i>Macrogyrus</i> sp.			1a			
Noteridae						
<i>Canthydrus bovillae</i> Blackburn			1a			
Dytiscidae						
<i>Eretes australis</i> (Erichson)		1b		1b		
<i>Homeodytes</i> sp.		1b	1b		1b	
<i>Hydroglyphus godeffroyi</i> (Sharp)	1a			1a		
<i>Hydroglyphus grammopterus</i> (Zimmerman)		1a				1a
<i>Hyphydrus</i> sp.				1b	1b	1b
<i>Laccophilus clarki</i> Sharp			1a	1a	1a	
<i>Laccophilus sharpi</i> Regimbart					1a	
<i>Laccophilus</i> spp		1b		1b		1b
Dytiscidae sp. A		1b	1b			
Dytiscidae sp. B				1b		
Hydraenidae						
<i>Paracymus</i> sp.			1a			
Spercheidae						
<i>Spercheus</i> sp.		1a	1a			
Hydrophilidae						
<i>Berosus debilipennis</i> Blackburn	1a					
<i>Berosus</i> aff. <i>ralphi</i> Watts	1a	1a				
<i>Berosus sadie/aquilo</i> complex					1a	
<i>Enochrus deserticola</i> Blackburn			1a	1a		1a
<i>Sternolophus immarginatus</i> d'Orchymont		1a				
Hydrophilidae sp.				1b		1b
Helodidae						
Helodidae sp.			1b			
Scirtidae						
Scirtidae sp.			1b			
Total	13	28	60	42	42	39



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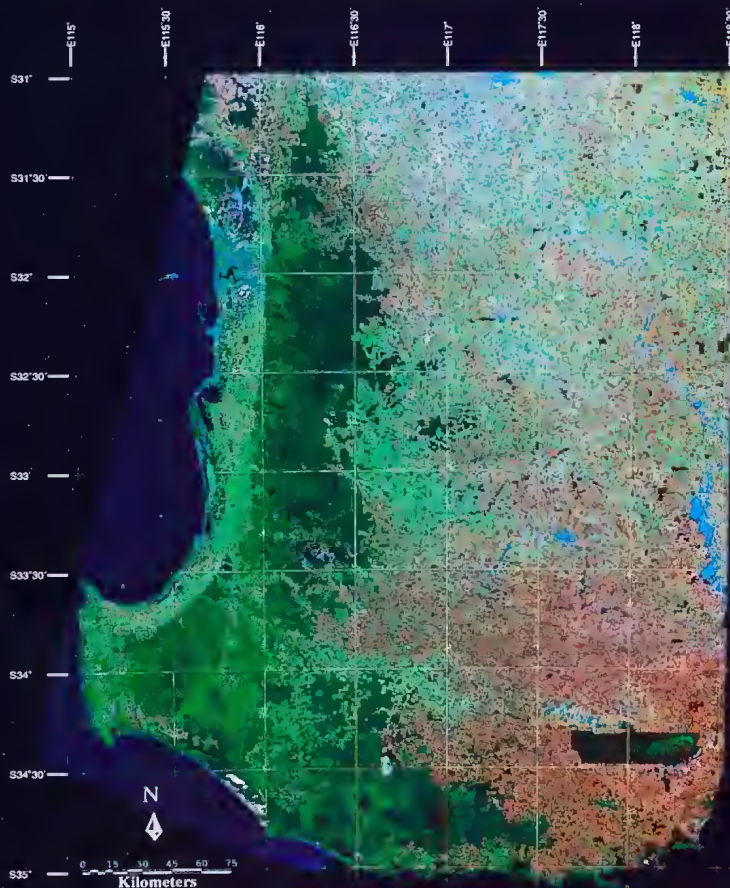
Symposium on the Design of Reserves for Nature Conservation in South-western Australia

Sponsored by
The National Biodiversity Council
and
The Centre for Ecosystem Management, Edith Cowan University
June 1995

Edited by P C Withers & P Horwitz
for
The Royal Society of Western Australia

South-West, Western Australia

Landsat TM Summer Mosaic, 1994-1996. Bands 1, 4, 7 in Blue, Green, Red.



Produced by: Remote Sensing Services, Department of Land Administration, Leeuwin Centre, Perth, W.A.

Landsat imagery provided by Australian Centre for Remote Sensing (ACRES), AUSLIG, Canberra, and digitally enhanced and produced by Remote Sensing Services, Department of Land Administration, Perth, Western Australia.

Symposium on the Design of Reserves for Nature Conservation in South-western Australia

Preface

This issue of the Journal of the Royal Society of Western Australia relates a series of papers, all presented at a symposium on the design of reserves for nature conservation in south-western Australia. The symposium was held in June 1995 at a time when there was (and still is) increasing public concern about nature conservation and conservation through reserves in the more densely populated, wetter parts of the south-west. The area of concern extends from the Swan Coastal Plain to adjacent forested ecosystems, where intense pressure exists for urban development, agriculture/horticulture, mining and timber extraction. There is a general perception that the scientific community needs to begin an informed debate, involving the general public, and this symposium was seen as an opportunity to air the issues.

The symposium coincided with a critical point in the forest debate in Australia. The Commonwealth Government, in an attempt to avoid perennial protracted disputes over woodchip quotas and forest reservation, engaged several prominent Australian forest ecologists to prepare selection criteria for reserves as a broad benchmark to preserve biodiversity, old growth and wilderness values of forests according to the aims of the National Forest Policy Statement (1992). A report was published (Commonwealth of Australia, 1995) which recommended, amongst many other criteria, that each forest community in Australia should have at least 15% of its pre-1750 extent reserved. Could this figure be sufficient to ensure the long term security of biodiversity in Australia's forests, or any other ecosystem?

The symposium was organised because of concern that any Australia-wide approach might not take into account the particular vagaries of south-western Australian biogeography. It was sponsored by the National Biodiversity Council and the Centre for Ecosystem Management at Edith Cowan University. Speakers were invited to cover a broad range of topics relevant to reservation of biodiversity, to ensure that a more comprehensive scientific knowledge on biodiversity in various landscapes of the south-western part of the continent could be accessed as part of the debate.

The Symposium was opened by the Hon Peter Foss, then Minister for the Environment in the Western Australian Government. In his speech the Minister suggested that scientists concerned with the conservation of biodiversity should direct their priorities to the wheatbelt of Western Australia rather than to the higher rainfall areas. The question arises: are scientific concerns for the management of urban or forested landscapes in Western Australia unfounded, misplaced or of a lower priority? One response of symposium delegates was that the wetter parts of the south-west must never be allowed to become degraded like the wheatbelt region, and that environmental degradation could be averted if early warnings from scientists are promptly considered.

Scientists' concerns about the wheatbelt date back to the early part of this century. Warnings about the consequences of clearing native vegetation for both water

quality and nature conservation have been sounded by scientists and naturalists for at least 70 years, but it is only now that such warnings are beginning to be heeded, and only in part. Many scientists take the view that the current management of south-western Australian forests and coastal plains requires immediate attention, much like the wheatbelt did 70 years ago. Indeed, forest and coastal ecosystems might also provide refugia for wheatbelt biota, as well as the unique biota which persist in these relatively moist environments.

The articles in this issue present perspectives on reservation of the wetter landscapes of south-western Australia. They include an historical review (Rundle), an overall assessment of the amount of reservation compared to other parts of the state (McKenzie *et al.*), and assessments of reservation status of biota from the viewpoint of taxonomic groups (Wardell-Johnson; BY Main), habitats (Trayler *et al.*) or ecosystem dynamics (Hobbs). An overview of forest reservation is the final paper presented (AR Main).

The area of focus was that bounded by the 500 mm isohyet, approximating Beard's (1982) Darling Botanical District. Another scheme includes three bioregions equating to Beard's (four) botanical subdistricts, namely the Swan, Jarrah Forest, and Warren Bioregions of the Interim Biogeographic Regionalisation of Australia (Thackway & Cresswell 1995). Alternatively, Hopper (1992) considered that the 800 mm isohyet (High Rainfall Zone) was a meaningful biogeographical boundary, and matching this closely is the Environmental Protection Authority's Reserve Systems of Western Australia. All four schemes are mentioned in papers in this issue (see Figure over), and a Landsat image of the south-west is presented as a frontispiece.

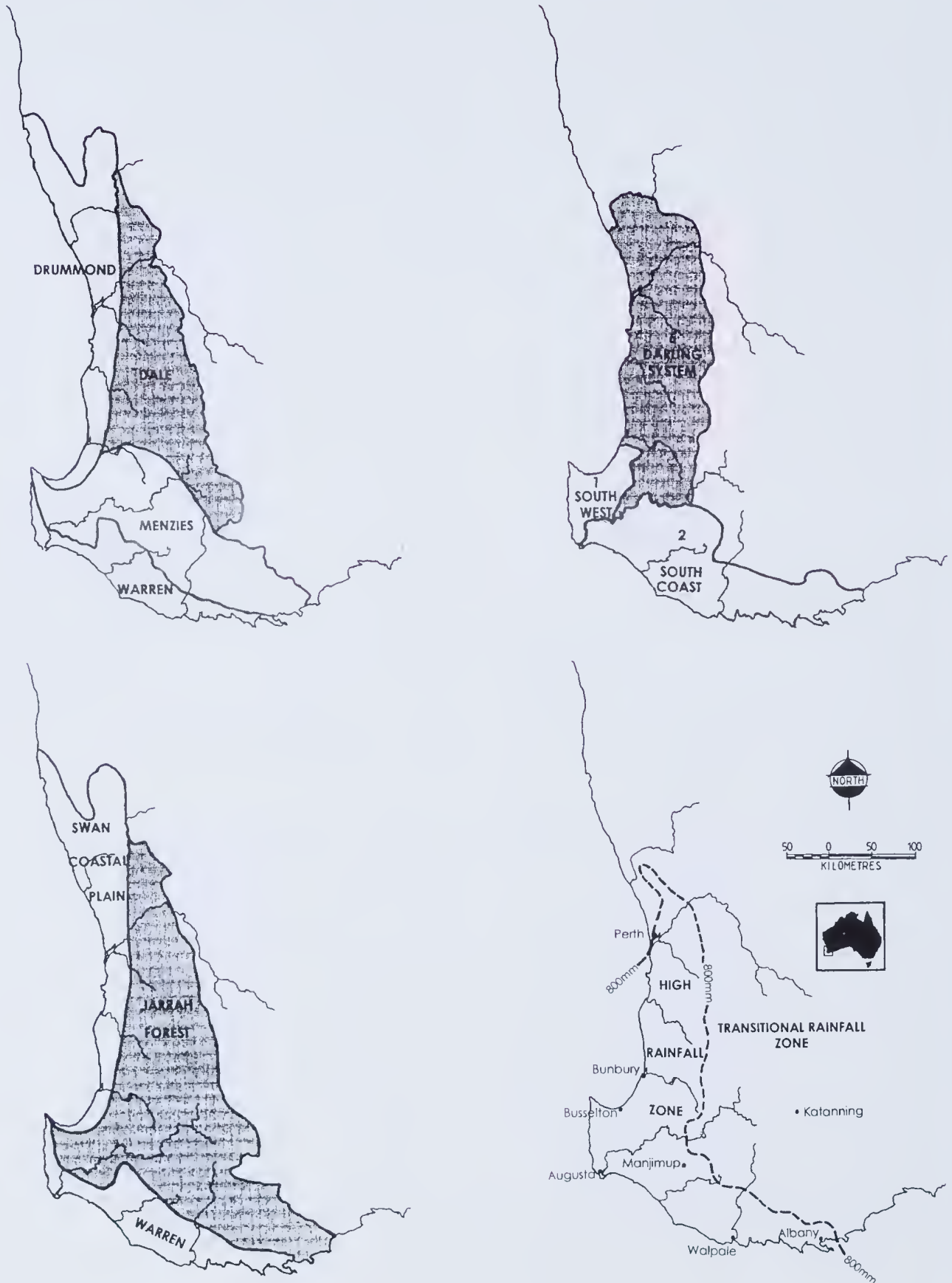
In 1973 the Royal Society of Western Australia published a special edition which reviewed the current knowledge of the south-western Australian environment. In his Preface to that volume, the Honorary Editor (AJ McComb) referred to the role of this Society and its Journal to provide a forum whereby information could be collated and made accessible to residents of the State. We are pleased to contribute to this tradition.

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Dr Pierre Horwitz
Symposium Convener, and Honorary Co-editor

Four biogeographical schemes referred to in papers in this issue. In clockwise order starting from the top left; Beard's (1982) Darling Botanical District (with four subdistricts); the Environmental Protection Authority's reserve systems 1, 2 and 6 which cover the wetter south-west; Hopper's (1992) High Rainfall and Transitional Rainfall Zones; and the three bioregions from the Interim Biogeographic Regionalisation of Australia (Thackway & Cresswell 1995).



History of conservation reserves in the south-west of Western Australia

G E Rundle

WA National Parks and Reserves Association,
The Peninsula Community Centre, 219 Railway Parade, Maylands WA 6051

Abstract

Focusing on the Darling Botanical District, reservation in the south-west of Western Australia largely involves the forest estate. The remaining natural bushland today is mainly reserves of State forest and so further opportunities to create new national parks or nature reserves of any significance would generally mean converting a State forest reserve to some other sort of conservation reserve. Thus, the history of Western Australia's State forest reservation is important.

The varied origins of some of the region's well-known and popular national parks are of special interest. Their preservation as conservation reserves generally had little to do with scientific interest and a lot to do with community pleasure in the outdoors and scenery. Their protection from early development had little to do with the flora and habitat protection needs that are the focus of these Symposium proceedings. Factors such as lack of shipping access, the discovery of glittering caverns, and the innovation of excursion railways were involved in saving the day. In contrast, the progressive reservation of State Forest was a hard slog by an insular Forests Department against many opponents.

The creation of a comprehensive system of conservation reserves in this part of Western Australia is an on-going modern phenomenon with continued wide popular support. While there are controversies concerning forest reservation and the conservation of urban bushland, these largely involve matters of detail over particular pieces of land. However, remaining unresolved is controversy over State forest management which might impact upon strategic wildlife habitat. Management of State forest for multiple uses, including ecologically sustainable timber production and wildlife values, is adopted Government policy.

Introduction

Geographical context

The Darling Botanical District is generally synonymous with several significant natural attributes, including the high rainfall area (over 500 mm per annum) of Western Australia's south-west, and a zone of active streams and rivers, whereas the hinterland beyond is largely characterised by more arid conditions and uncoordinated drainage (Beard 1981).

Tall forest and tall woodland formations are confined to this part of the State and today comprise the dominant area of uncleared land. Of particular significance, it forms a large block of generally contiguous reserves of State forest. Created originally to support an export saw milling industry, today's forest management emphasis is on multiple use objectives of which catchment protection for water supply is arguably the most important.

West of the forest of the Darling Plateau, the fringing narrow Swan Coastal Plain is the earliest part of Western Australia that was extensively settled by Europeans. The bulk of this land was released into private ownership within the first hundred years of this settlement, with little consideration given to a need for bushland conservation. Converting uncleared remnants into conservation reserves there now usually requires the buying back of land that is in private ownership. There are situations

where there is added justification to do this when key ground water aquifers within the deep sands of the coastal plain need to be protected from the likelihood of pollution arising out of urban and agricultural development.

Administratively, the Darling Botanical District is also closely synonymous with several regions. These include the Environmental Protection Authority's (EPA) Systems 1, 2 and 6 collectively, which were designated in the early 1970s as part of a State conservation reserve assessment project (Ride 1975). State forest and the bulk of Western Australia's conservation reserves are today managed by the Department of Conservation and Land Management (CALM). The contiguous CALM regions of Southern Forest, Central Forest and Swan (formerly Southern Forest and Metropolitan Regions) are also basically confined to the Darling Botanical District.

Historical context

Over the past 120 years of history of Western Australia's conservation and forest reserve systems, there have been a number of Acts of Parliament passed and consolidated that have enabled;

- land (and waters) to be reserved,
- the provision of degrees of security for reserves against alienation for other purposes, and
- the management of reserves by specific agencies.

Over that period, the principal reserve management agencies have also had name changes, or have been replaced by another agency. The phases of forest and conservation reserve establishment can be summarised as follows:

- **Colonial Era: 1829–1889** Little was appreciated about the relationship of wildlife and habitat dependence, and the need was not seen for conservation reserves in a region which was still relatively undeveloped and unpopulated. Little interest was shown in protecting forest resources.
- **Early Self-Government: 1890–1929** In this brief 40 year period, gold rushes to the Murchison and Eastern Goldfields led to a rapid population increase via immigration and the promotion of railway development. In turn, both events stimulated the creation of recreation-based reserves (e.g. today's John Forrest and Leeuwin-Naturaliste National Parks).

A shift away from labour-intensive shallow fossicking to mechanised deep mining on the goldfields diverted development interest to agricultural expansion, especially in the forested 'south-west' (Darling Botanical District) and adjoining Wheatbelt, aided by a developing railway network.

The emphasis on conservation reserve selection remained oriented toward scenic landscape and recreation with new national parks being created at Pemberton and Nornalup. The need for strategic reserves for habitat protection was ignored, particularly in the Wheatbelt.

At the same time, there was rapid expansion of the timber industry, but also a growing awareness that better protection and management was needed for the forest estate. This need was enhanced by the utilisation of some forested catchments for water supply dams. A significant step was the passing of a Forest Act in 1918, the formation of a Forests Department, and the establishment of a million ha of State forest reserves by 1929.

- **Modern Era: 1930–1969** While there was little change over the period of the Great Depression and World War II, post war reconstruction brought major change. Rapid agricultural, mining, industrial and urban expansion brought an awareness of the need to secure more natural areas for habitat protection and as 'refuges' for passive recreation. There was also an emerging realisation of the need for professional and well-resourced management of reserves, and lobbying for improvement was a feature of this period.

Characteristically, it was an era of land-use conflict between competing developments, and between development and conservation. The few attempts at conflict resolution by Government were not particularly successful. While State forest reservation made some hard-fought gains against agricultural expansion, there was only a slow improvement in the conservation reserve estate. However, the scientific community, mainly through the Australian Academy of Science and the Royal Society of Western Australia, stimulated community interest in the need for the establishment of an adequate conservation reserve system.

Towards the end of this period there was also an

emerging change in forest management toward more intensive productivity, both for timber and broader community benefits of catchment management, recreation and habitat management.

- **Present Era: 1970–1995** There was State Government acknowledgment that sound grounds existed for expansion of Western Australia's conservation reserve system, and also the need for better conflict resolution processes. During this recent period the conservation reserve system dramatically increased.

This period has also been notable for its forest management controversy. This situation developed as the wider community began to appreciate that production management for timber was focussed on the manipulation of the natural structure of production forests. Up to this time, there had been general acceptance that forest production management had little impact on wildlife habitat.

There has been some rationalisation between conflicting land uses and also rationalisation of reserve management agencies through the creation of the Department of Conservation and Land Management. Overall, reserve management has become better resourced during this current period although not necessarily adequately resourced. Unresolved conflicts remain. Mechanisms to deal with many of these are absent or do not have broad acceptance.

Colonial Years (1829 - 1889)

The first 60 years

Although the first European settlement in Western Australia was established at King George Sound (Albany) in 1826, it was an outlier of the New South Wales colonial administration. In practical terms the first settlement was on the Swan River in 1829, under the charge of Captain James Stirling as Lieutenant Governor. Early land development was based on garden, orchard and agricultural plots close to homesteads, spread along the Swan and Canning estuaries and lower river reaches on the coastal plain near Perth. However, pastoral land use expanded in the 1840s, from north of Perth to the Gingin area; northward from the already settled Avon Valley district to the Victoria Plains and New Norcia-Moore River areas; and southward from the Avon Valley, following the inland route between Williams and Albany (Cameron 1981). This development avoided the heavily timbered country of the main forest belt.

For more than half a century the colonists were surrounded by plentiful virgin country, and early conservation regulations were aimed at protecting fauna rather than the habitat upon which the wildlife depended. For example, the early Game Acts had the intention of protecting kangaroos and other fauna to meet the economic and sporting needs of the settlers, and to ensure continuance of Aboriginal food sources.

The first reserves for conservation purposes were set up under the Land Regulations for the Colony of 1872. Another set of Land Regulations enabling the creation of

reserves was promulgated in 1887, and it was not until a new Land Act was passed in 1898 that previous land regulations were consolidated. Perth Park (now Kings Park) was the first of the State's significant bushland reserves to be created under the early Land Regulations. The first part of this Park was established on the suggestion made in 1871 by Governor Sir Frederick Weld. Following gazettal of the 1872 Land Regulations, he was able to approve the setting aside of 432 acres (about 200ha) for the purpose of "public park and recreation" on October 1, 1872.

Of interest, 1872 was also the year that Yellowstone National Park had been set aside by the US Congress, although the national park idea had an earlier beginning than that of Cornelius Hedges for Yellowstone in 1870. In Europe in 1810, the English poet, William Wordsworth, put forward a notional idea for the Cumberland Lake District as being a 'sort of national property.' Some 40 years before Yellowstone, the American artist George Catlin in 1832 conceived a similar concept for the Dakota prairies and its plains Indians providing 'a nation's park'.

Towards self government

In 1880, the colony of Western Australia was granted representative government, a step toward eventual responsible government (*i.e.* self-government). Towards the end of the decade, when the population was about 40 000, the colony was ready to assume responsible government, and this move was spearheaded by Sir John Forrest, then Surveyor General and Commissioner of Crown Lands, and a Member of the colony's Legislative Council. Land policy and administration was the principal issue driving self government and Forrest's report to the Legislative Council in 1889 on land policy was critical of development constraints while an Imperial Government in London still maintained a fair measure of control over the administrative affairs of Western Australia (Forrest 1889b).

In the following year, 1890, a *Western Australia Constitution Bill* was presented by the Imperial Government to the House of Commons, aimed at granting self government to the Colony. A Select Committee of the Commons had been appointed to inquire into the proposal for this remote and little-known colony, and it took evidence from its Governor, Sir Frederick Napier Broome, who had travelled to London. Forest conservation in the Colony was only briefly covered by questions from the Select Committee and the Governor's recorded answers are a fair assessment of the situation at that time (Anon 1890);

- *Is there any system of forest conservation; under what rules are the forests allowed to be worked?*

There has been some attempt at it, but forest conservation is still in a very rudimentary state. There was an inspector of forests appointed some time ago, and there were some regulations made under legislation in connection with the matter, but they have been insufficiently carried out, and forest conservation can hardly be said to be initiated yet. The fact is that the whole of the south-west division is so thickly covered with forests that the great desire of everybody is to get rid of as many trees as they possibly can. Of course the day will

come, and even now is, when the forests ought to be preserved from waste.

- *Practically, are people allowed to cut wood as they like?*

No, that is dealt with in the Land Regulations; they must obtain licences and pay fees.

- *But are they allowed to cut what trees they like?*

Yes there is very little restriction upon them; not so much as there ought to be, I think: some system of working the forests carefully and not wastefully ought to be introduced.

It is interesting to note that early Timber Regulations under Western Australian colonial land legislation, and later that of its own Parliament, restricted timber felling to extremely large trees, the dimensions of which would now be uncommon, particularly in jarrah forest.

A starting point

Since late colonial times Western Australia has been divided into several Land Divisions in which varying land release and settlement policies could be applied. It had long been thought that agricultural potential was basically confined to the South West Land Division, which initially extended from the Northampton area in the north through Cunderdin, to Bremer Bay near Albany in the south. It was originally intended that broadscale releases of land into private ownership (*i.e.* freehold) would be restricted to this Division and that land development elsewhere would be covered by leases of land retained in Crown (public) ownership. On the eve of self government in 1890, the South West Land Division was described (Forrest 1889a) as follows;

This division contains 67,000 square miles [194 000 km²], and comprises the most temperate part of Western Australia. It is that portion of the Colony first settled, and in which about 39,000 out of the whole population of 42,300 reside.

The South-Western corner is heavily timbered, and is fairly well watered and capable of supporting a large population. It is generally an undulating country, and, with the exception of the Darling Range and a few other small ranges, has no extensive mountain ranges.

Numerous rivers enter the coast within this division, but they are all very short and merely drain the country within 100 miles [160 km] of the coast.

The work and expense of clearing the land has proved very laborious and very great, but, when the ground is properly prepared, a fair crop can be depended upon.

In its natural state it takes about 10 acres [4 ha] to keep a sheep, but with clearing and improving it will keep a sheep to two acres [0.8 ha], and in choice places a sheep to one acre [0.4 ha].

It is estimated that at the present time there are depasturing, within this division, 866,229 sheep, 52,415 cattle, and 29,786 horses.

The climate is very good, and the rainfall varies from 14 inches [350 mm] in the northern and inland portions, to 45 inches [1125 mm] in the southern portion of the division.

The area leased from the Crown for pastoral purposes at the present time is 24,514 square miles [63 450 km²].

Early Self-Government (1890 - 1929)

Perth Park (Kings Park)

Originally created in 1872, Perth Park was enlarged in 1890 at the suggestion of Sir John Forrest, who by that time had become Premier of Western Australia. In 1895, a management committee for the Park was formed and Forrest became its first President. Under his patronage, two important pieces of legislation were passed to both enable management of the Park and to provide security against it being alienated for other purposes. Both pieces of legislation were applicable to other reserves.

The *Parks and Reserves Act* was passed in 1895, enabling the government to create boards of management for reserves and providing such boards with powers to manage the areas vested in them. Under this legislation, Sir John Forrest's management committee became the Perth Park Board. In 1899, the *Permanent Reserves Act* was passed. It too was initiated by Sir John Forrest to provide Parliamentary protection against the alienation for other uses of "Public Parks". However, his Parliamentary colleague and also a member of the Perth Park Board, Sir Winthrop Hackett, had the original Bill changed in the Legislative Council to provide for the concept of classifying reserves as A, B or C, regardless of their purpose, and this was passed.

Under Hackett's concept, class A reserves became the most secure, requiring an Act of Parliament to vary their boundaries, change their purpose or cancel them. B and C class reserves could be changed without the need for Parliament's consent, but Parliament had to be given an explanation in the case of B class reserves.

Shortly afterwards, in 1901, the name of Perth Park was changed to Kings Park. In its short history to that point the Park had stimulated the production of the necessary primary legislative tools to protect and manage reserves - security of purpose, and the appointment of statutory managers with powers to manage (Australian Academy of Science 1962; Christensen 1992).

Early forest reservation

During the 1890s, forest conservation and management in the southern Australian states followed somewhat parallel lines. In fact, Western Australia's first Conservator of Forests, John Ednie-Brown, became a common link in the efforts of several states to come to grips with forest conservation (Powell 1976). Forest reservation and timber cutting initially came under the jurisdiction of colonial land administration agencies. However, forest management needs conflicted with the primary purpose of these "Land Departments", that of promoting land settlement and clearing policies for agricultural production.

Whilst allowing timber to be cut aided settlers in taking up the cleared land, retaining forest land as a sustainable resource was seen by Australian land administrators as "locking up" the land. In Victoria there were proposals to establish "State forest" as early as 1865, but none of the several Forest Bills presented to Parliament between 1879 and 1892 became law. George Perrin, Victoria's first Conservator of Forests, continued to head a small division within the Lands Department; he died in office in 1900 and was not replaced for some years.

Victoria at last proclaimed a *Forest Act* in 1907, and a new Conservator (A McKay) was armed with new powers.

Before becoming Western Australia's first Conservator of Forests in 1896, John Ednie-Brown had been South Australia's first Conservator of Forests in the late 1870s and subsequently moved to NSW in 1889 to become that state's Director-General of Forests. Like George Perrin in Victoria, when Ednie-Brown came to Western Australia he headed a Woods and Forests "Department" (i.e. Division) within the Lands Department. Ednie-Brown's untimely death three years later also prevented any real advance in forest conservation and management in Western Australia, and as in Victoria no trained forester was appointed to replace him for many years. (Forests Department 1969; Underwood 1991).

John Ednie-Brown recorded the following (Fraser 1903);

I am, never the-less, pleased to be able to state that the forest's of Western Australia are yet practically unharmed for all purposes of successful conservation and ordinary thinnings and clearings of the matured timber...

The forests are nature's gift, and should be looked upon and dealt with accordingly, as an inestimable inheritance of great commercial and climatic value; besides much of the land upon which the best timber grows is, as a rule, of little or no value for agricultural purposes, and I maintain, without fear of logical contradiction, that what is now upon it is the very best kind of crop that will ever be seen there. To destroy it therefore, for the sake of a few more blades of grass, is suicidal and reprehensible in the extreme.

At about this time, a Royal Commission into forestry matters in Western Australia had been held and a Forest Advisory Board established to consider applications for timber cutting concessions. Without specific forestry legislation under which forested land could be reserved, protection against agricultural selection in Western Australia was afforded by the creation of numerous reserves under land legislation, generally having the purpose of "Timber: Government Requirements". By 1910 a dozen or so of these existed (Dept. Lands and Surveys File 2507/93 Vol. 3), totalling 261 095 ha and were administered by the Woods and Forests "Department" of the Lands Department, headed by an Inspector, using Timber Regulations promulgated under land legislation. However, these reserves were Class C and therefore insecure against disposal for farm release.

South Dandalup Nature Reserve

Focused on the catchment of the South Dandalup River between Pinjarra and Bannister, the former "South Dandalup" nature reserve is sometimes also referred to as the "Pinjarra Wildlife Reserve" or "Bannister Flora and Fauna Reserve". It was Western Australia's first nature reserve, was large at 64 000 ha, had a scientific basis (for that time) to its creation, and was subsequently cancelled to permit timber cutting and orcharding.

In the 1880s scientific professionalism in Australia was increasing, and in 1888 the Australasian Association for the Advancement of Science was formed. The Association held a meeting in Adelaide in 1893, and a con-

cept was developed for establishing conservation reserves within Australia. At this time, there was a scattering of reserves close to capital cities that were based on scenic landscape and associated recreation interest. However, the Association's concept was oriented toward habitat protection, with the reserves controlled by local honorary trustees and supported by Government grants.

The Association decided to approach the Western Australian Government to have Rottnest Island, near Perth, and the Abrolhos archipelago, near Geraldton set aside for this purpose. These suggested sites were not set aside, but Premier Sir John Forrest invited Bernard Woodward, the Director of the Western Australian Museum, to select another site; he chose the South Dandalup forest area.

At the time, Bernard Woodward considered this area to be difficult heavily-forested country, and so nobody was seeking it for agricultural development. The timber industry was then focussed further north at Jarrahdale and Canning Mills. The selection of the South Dandalup area was supported by the Premier and the reserve for "Flora and Fauna" was gazetted in 1894. It was 64 000 ha in extent, and was bound in time to cause problems in "locking up" so much land and timber close to settled areas. Unfortunately, in 1894 the legislation that eventually afforded Perth Park its protective management and security of purpose had not been passed. Had it been possible to invoke these provisions immediately, the fate of the "South Dandalup" nature reserve might have been different.

Within a few years of its creation, attempts had started to have the timber in the nature reserve made available for commercial exploitation. John Ednie-Brown, the new Conservator of Forests, for example, commented in a memo to the Minister for Lands in 1897 (Lands Dept. File 2507/93);

There is some very fine timber upon this reserve but it is simply going to waste and should certainly be utilised.

Sir John Forrest apparently withdrew his previous support for the reserve, and agitation for timber cutting and agricultural release for orcharding in valley land continued. In 1901, conditional permission to cut timber on the reserve was granted. Woods and Forest staff subsequently proposed cancellation of the reserve, causing Woodward to intercede. In 1902 he sought legislation to have the reserve vested in Trustees, but this was rejected by Cabinet, which instead proposed that it be opened for timber cutting. In the following year, 1903, a Royal Commission on forestry recommended that further timber cutting in the nature reserve should cease, but this too appeared to have had little affect.

By 1907, various attempts to cancel or reduce the reserve's size had been warded off, but a permit to cut timber had been granted to a large milling concern, Whittaker Bros. On May 28 in 1907, Bernard Woodward delivered a lecture to the West Australian Natural History Society (forerunner to today's Royal Society of Western Australia) and chose as his topic "National Parks and the Fauna and Flora Reserves in Australasia". In his talk, Woodward gave an account of the movement for conservation reserves in the various Australian states and New Zealand, and reported on the unsatisfac-

tory situation of the South Dandalup nature reserve. Arising out of the ensuing discussion, the Society resolved to petition the Governor to have the nature reserve declared a national park, and be vested in trustees to manage.

The petition was conveyed by Governor Sir Frederick Bedford to the Premier, J Moore, in August 1907. Premier Moore sought a report on the matter from the Lands Department. Officials, including the Surveyor General and Acting Inspector General of Forests, opposed the idea of vesting the reserve in trustees for a national park as it would "lock up" a large tract of valuable jarrah forest for the "mere preservation of flora and fauna". By this time, a number of water catchment reserves in the forest area further north, between the York Road and Jarrahdale, had also been declared under land legislation, totalling over 100 000 ha. It was therefore proposed to set apart the protected Mundaring Catchment Area as a reserve for the protection of "Native Flora and Fauna". However this never occurred and the purpose of the South Dandalup nature reserve itself was converted to "Timber - Government Requirements" in 1911, and subsequently became incorporated into State Forest no. 14 (Dept. Lands and Survey File 2507/93, Vols 1 and 2; Woodward 1907; Australian Academy of Science 1962; Conservation Council 1980; Christensen 1992).

South-west cave reserves

The existence of numerous caves in the Leeuwin-Naturaliste area had been known by early residents since at least the 1870s. As some of these became more widely known and visited, there was some local concern regarding the destruction of some of the glittering formations they contained. On the urgent representation of Mrs John Brockman, the Minister for Lands, George Throssel, commissioned an exhaustive survey and inventory to be made of the district's caves. Of particular interest is the approach taken to do this.

In 1894, the first step was to declare a reserve of 6 600 ha (Reserve 2565) over vacant Crown land in the Margaret River-Augusta area. This was designed as a holding action to prevent further farmland releases until the cave survey and inventory had been completed. During the next several years, a Lands Department team under the Chief Inspector of Lands, Charles Erskine May, explored and catalogued the caves.

Erskine May presented his report to the Government in 1900, in which numerous caves and the glittering decorations were eloquently described. By this time Western Australia had experienced the main goldrush era and the majority of its population was now residing in major towns in the less-hospitable Eastern and Murchison Goldfields but linked to Perth by an efficient rail system. In his report, May saw the development of the caves as contemporary resort attractions, with the provision of a "sanatorium" on the Margaret River as a 'national' opportunity of fostering health and recreation (Erskine May 1900);

"..... to the goldfields especially, the Margaret River should be the Blue Mountains of NSW, the Derwent of Tasmania or the Lakes of New Zealand when they are making a holiday".

The key to this concept was the existing rail link from Perth to Busselton, providing reliable and comfortable transport from the goldfields as well as from Perth. In 1901 a Caves Committee was set up to recommend on the implementation of Erskine May's report. This resulted in the cancellation of the original 'holding' reserve and the simultaneous gazettal of a dozen smaller cave reserves in 1902. Unlike the besieged "South Dandalup" nature reserve (which had been gazetted before enactment of the Permanent Reserves Act), all were afforded Class A security and vested in the Committee as a properly constituted board of management under the *Parks and Reserves Act*.

Caves House at Yallingup was developed as a guest house by the Board, and nearby Yallingup Cave was provided with electric lighting to prevent formations from being damaged by other smoke-producing forms of illumination. Caves Road was constructed to link about a dozen "fully stepped and staired" caves to the accommodation centre at Yallingup and the railhead at Busselton. From Busselton, horse-drawn conveyances initially took visitors to their accommodation and, later, motor vehicles were used. A marketing innovation was the issue of "single cost" excursion vouchers that covered both the rail and road journeys, accommodation and cave entrance fees. Subsequently, the Caves Board had the caves at Yanchep vested in it and it established camping and tent-hire facilities in that reserve.

The Caves Board existed until 1910, after which it ceased to function. Responsibility for the cave reserves was transferred to the State Hotels Department in 1914, which had responsibility for running hotels in wheatbelt "frontier" towns to accommodate the many prospective land seekers, agents and commercial travellers active during that era. When the Department was closed in 1960, administration of the cave reserves reverted back to the Lands Department. Sometime later the reserves were passed on to the State Gardens Board. This Board had been formed in 1920 to manage a number of small parks and gardens within Perth's city precinct but soon found itself responsible for a number of national parks and other unvested bushland reserves, often distant from Perth. The cave reserves eventually became the core of the Leeuwin-Naturaliste National Park (Erskine May 1900, 1903; Australian Academy of Science 1962; Fraser, 1903; Mulcahy *et al.* 1988).

John Forrest National Park

Prior to 1895, the Eastern Railway to Northam and its link to the Great Southern Railway to Albany, passed through the Darling Scarp south of Greenmount and was routed via present-day Darlington and Mundaring. A better grade was subsequently located via the Jane Brook valley, north of Greenmount, and this alternative route was opened in 1895. The genesis of John Forrest National Park is directly linked to this new railway, and the reliability and comfort that rail travel provided.

Near the point where the railway entered the valley and Jane Brook leaves is the popular Rocky Pool. This was only a short downhill walk from the new Swan View Railway Station. The first part of today's national park was set aside here in 1895 in the form of two reserves, one for "Public Park" and the other for "Public Utility". In 1900 a more extensive reserve for "Parkland"

was created upstream of Rocky Pool and excursion sidings constructed. A year later in 1901, the "Public Utility" reserve near Rocky Pool was also converted to the purpose of "Parkland".

While official correspondence and plans in 1901 referred to the area as a "national park", it was not until 1926 that the main reserve had its purpose changed from "Parklands" to "National Park and Native Game". For quite some time afterwards the Park was referred to as "The National Park". At one time, all three reserves were vested in the former Greenmount Road Board, but came across to the newly formed State Gardens Board just prior to the Great Depression. After World War II, the State Garden Board was transformed into the original National Parks Board (and like the Kings Park Board, also operated under the Parks and Reserves Act), to be subsequently replaced by a National Parks Authority in 1976 (operating under its own Act), and in 1971 the Park was officially named "John Forrest National Park" (Australian Academy of Science 1962; Dept. Land Administration reserves database).

Other "Hills" attractions close to Perth had similar histories relating to rail accessibility, although not all sites were available for parkland reservation. When constructed, Mundaring Weir was an immense attraction and the construction railway became an excursion railway to the site. Subsequently motor transport replaced this, and it was the drive to Mundaring Weir via Kalamunda that was later to promote early legislation for protecting wildflowers. The road access from Gosnells railway station to Victoria Reservoir was also promoted as a tourist drive. Further south, the Serpentine Falls also had an early tourist history with people initially travelling via the railway to Mundijong. In 1911, it was reported that "trainloads of excursionists" were visiting the falls every wildflower season (National Parks Authority 1992).

Pemberton National Parks

The two principal national parks that were originally created in the karri forest near Pemberton are part of several reserves collectively referred to as the "Pemberton National Parks". Following John Ednie-Brown's death while the State's first Conservator of Forests, Mr V G Richardson, an Inspector of Forests, held the position of Acting Conservator.

The first national park in this area was proposed by Richardson in 1901. The Acting Conservator sent a file minute to his superior, the Under Secretary for Lands suggesting that a "fine patch" of karri forest on the Vasse Road "be reserved as a sort of National Park, so as to allow posterity to see what the virgin karri forests were like". Cecil Clifton, the Under Secretary of Lands, was enthusiastically supportive and hoped that the selected patch would have "some really noble trees on it". Richardson then charged Forest Ranger H S Brockman to select one or two patches of forest, including Beedelup Falls if possible, up to nine or ten thousand acres (about 4000-4500 ha) in area "as it would be inadvisable to lock up too large an area of good land as a Forest Reserve."

Within 20 days of Richardson making the original suggestion to Cecil Clifton, Brockman had returned a map showing two blocks of karri forest that should be

reserved as National Parks, Beedelup and Warren. They were subsequently gazetted as timber reserves rather than as national parks, probably so that the Acting Conservator of Forests could maintain a protective interest. However, not being 'A' Class, pieces of both reserves were progressively whittled away to provide farm grants and by 1909 parts of the remainder were sought for timber cutting and timber railway routes by the State Sawmills Department. The Under Secretary for Lands finally settled this insecure situation by having the boundaries of the reserves rationalised to allow passage of the timber railways, having both reserves include replacement areas of forest, and persuading the Government to secure them once and for all as Class 'A' national parks to protect the original concept initiated by the Acting Conservator of Forests. Thus, both national parks became a reality in 1909 after being progressively shifted from their original locations (Dept. of Lands and Survey File 74/01).

The Forests Department

A federation of Australian self-governing States was created on January 1, 1901. Forestry, however, does not seem to have been considered very seriously in the conventions leading up to federation and forest ownership and management remained with the individual states rather than being transferred to the national government. In general, although the timber industry was an important part of the economics of the States, scientific forestry was not vigorously pursued before 1910 in Western Australia, Tasmania or Queensland.

The first Interstate Forestry Conference was held in 1911 and academic forest training facilities were being established in some states. Scientific forestry advanced even further in 1914 when the British Association for the Advancement of Science convened a special conference in Australia (Powell 1976). One of the visitors was D E (later Sir David) Hutchins, a leading forester with wide experience in India and South Africa. Hutchins was subsequently invited to report on the forests of each state and this report was published in 1916 by the Western Australian Government (Hutchins 1916), indicating the government's deep interest at this time in coming to grips with forest management in Western Australia. Professional forestry was given a boost by Hutchins' activities and his report became the basis of a new move towards an Australia-wide management policy.

In Western Australia, in 1916, the State Government appointed C E Lane Poole to be the new Conservator of Forests. A graduate of a highly regarded European forest training centre and with subsequent colonial forestry experience, Lane Poole was primarily responsible for drafting Western Australia's *Forest Act* (Forests Department 1969; Underwood 1991) and drew on parts of Hutchins' report. Passed in December 1918, the Act received the royal assent in January 1919 and a new Forests Department was formed, separate from the Lands Department. Of additional importance, the Act enabled State forest and timber reserves to be created under its own provisions, with 'conveyancing' processing conducted by the Forests Department itself, instead of using Land Act provisions and Lands Department officials.

One of the first tasks of the new Forests Department was to survey and classify Crown lands for their timber

potential. Although by 1921 close on a million ha of forested land had been classified for retention from agricultural development, reservation as State forest had become a slow process. The Government of the day still showed more interest in agricultural land settlement, and a number of farm settlement schemes had come into operation following the close of the Great War in 1918. These had the objective of settling returning soldiers and encouraging immigration from Britain. However, a change of government in 1924 resulted in substantial increases in State forest reservation. By the end of 1929, the centenary year of the founding of Western Australia, a million ha of State forest had been proclaimed. Amongst the first areas to be covered by declared State forest under the new legislation were the Mundaring and Perth water supply reserves, that were once considered for the additional purpose of nature conservation in lieu of the cancelled "South Dandalup" nature reserve (Forests Department 1969; Mulcahy *et al.* 1988; Underwood 1991; Christensen 1992).

From its earliest years, the Forests Department and its Conservator set about promoting the principles of forest preservation and management, and 'Arbor Day' was established as an annual institution. In 1920, the Department under Lane Poole published "Notes on the Forests and Forest Products and Industries of Western Australia", to present in 'popular form' information on the objectives of forest management. A second and enlarged edition was published in 1921, in which the silvicultural concept of "sustained yield" is explained (Forests Department 1921);

Forest Capital and Forest Interest:

The "capital" of a forest may be defined as the total amount of marketable timber it contains: the "interest" is the total annual growth of the trees: in other words, the percentage by which they increase in volume. In a forest in which a large proportion of the trees are mature or over-mature, the ratio of annual growth is relatively small; in the case of a forest which contains a large proportion of young and immature trees, the ratio of annual growth is relatively large. In a "natural" forest, that is a forest which has received little or no attention at the hands of a skilled forester, the annual growth is much less than is the case in a "cultivated" forest. In a "natural" forest there are to be found many imperfect trees - misshapen, fire-damaged, or otherwise defective and incapable of developing into trees suitable for milling purposes. In a "cultivated" forest all these imperfect trees would have to be removed, and the space they occupied filled with trees capable of developing into marketable timber. Forest cultivation, therefore, increases the yield of timber: in other words, increases the annual interest on the forest capital.

"A Primer of Forestry" was also produced and issued to schools through the Department of Education. The Second Edition of this work, published in 1925, describes the 'cultivation' of a natural (or wild) forest system to produce the so-called "normal" forest of centuries-old European tradition (Department of Education 1925);

The 'cultivated' forest already referred to is the ideal of modern scientific forestry. In France, Belgium, and Germany the whole of the forests are cultivated, and in other European countries the process of converting 'wild' or 'uncultivated' forest to 'cultivated' ones is proceeding

apace. In Australia, with the exception of certain plantations, mainly of exotic trees, the forests are still uncultivated, but in every State the process of conversion is being pushed on. The effect of cultivation upon a natural forest is to increase very materially the amount of timber which the forest can yield annually without in any way diminishing its productive power.

It was this concept of converting a natural forest ecosystem into 'younger' and greater wood-yielding production forests that primarily led to the environmental concerns of a future generation.

Karri National Parks

In the early days of the Swan River Colony, very little was known of the south coast region. Although the settlements of Albany and Augusta are amongst the State's earliest (1827 and 1830 respectively), both were established from the sea and their hinterlands and the coast between them was little known. Coastal landings were difficult due to cliffs, beaches with formidable breaking waves, and inlets with sand-barred mouths. Behind the coastline are lines of swamps and river inlets and estuaries, and a hinterland of heavy forest.

In 1830/31, an exploration party led by Captain Bannister attempted to determine a line that could be followed and developed as an overland route linking Perth to Albany. In the vicinity of "Nornor-up" (Nornalup) the party passed through forests of "blue gum". Bannister was amazed at their size (Cross 1833);

..... if others had not seen them, I should be afraid to speak of their magnitude; I measured one, it was breast high, forty two feet [14m] in circumference; in height, before a branch, 140 or 150 [about 50m] we thought at least, and as straight as the barrel of a gun.....

Some time afterwards, the existence of such forests of karri trees around Nornalup Inlet was confirmed by former sealers at Albany, and a syndicate of Albany residents chartered a boat to examine this potentially lucrative resource. However, while the forest of enormous trees was confirmed, so was the difficulty of shipping timber out of the shallow and barred estuary. In 1832 a party of sailors were sent in an open whaleboat to explore the little known coast inshore. They became stranded on Warren Beach when sheltering from a storm, and walked much of the future D'Entrecasteaux National Park coast to reach Augusta. A decade later, the naturalists James Drummond and John Gilbert attempted to reach Albany from Augusta (i.e. King George Sound and Cape Leeuwin areas, respectively). However, after spending several days in a bewildering maze of swamps in the Scott River-Gingalup Swamps area, they turned back to Augusta. None of these expeditions provided information that the region's timber and land resources could be readily exploited.

Later in the century Ferdinand von Mueller produced a report on Western Australia's forest resources which described the extent of karri forests near the Warren, Shannon, Donnelly, Walpole and Gardiner Rivers. He considered that karri timber would doubtless become important for the timber trade if inlets of the south coast wilderness, between Cape Augusta and Albany, could be developed for shipping. Development headed towards the south coast, in the vicinity of Pemberton

and Denmark, in the late 1890s, and it was railways that were used to access forest and to transport milled timber to ports at Bunbury and Albany. However, the forested Frankland and Shannon valleys posed problems for heavy-railway development, which would have assisted forest clearing for agricultural expansion. By the mid 1920s more and more of the forest in the region was being protected by State forest reservations. However, wider knowledge of the south coast region increased as the milling industry expanded. Group Settlement schemes based on dairying were established in some areas cleared of forest, sometimes by the wasteful process of tree ring-barking. Above all, the new popularity of the motor car and their adventurous owners meant that previously unvisited places were being promoted.

The 1924/25 edition of The Western Australian Tourists Guide and Hotel and Boarding House Directory, under the heading 'The Inlets and Rivers of the South Coast - A Great National Asset', stated (Government Tourist Bureau 1925);

The whole region is a succession of scenic beauties and desirable spots which offer innumerable attractions to the sportsman. Those who wish to make the best of the Inlet Country must camp out, and the only difficulty they are likely to experience is that of deciding where to pitch their tents in a district which presents so many favourable situations. Among the rivers and inlets one finds a country that is unhackneyed, for its delights can be enjoyed only by those who are prepared to camp out and to put aside for a time the formalities of city life. But none can go there without benefit from a health point. It is proposed that a big area adjoining Nornalup shall be reserved for all time as a National Park and tourist resort, and the proposal is a wise one. Meantime, in that marvellous country Nature is still primitive, and that fact alone is a powerful lure to many.

The original national park was referred to as the Nornalup National Park, after the name of the inlet on which it was focussed, and adjacent town. A series of contiguous reserves for "National Park" were first set aside here in August 1924, with some small additions in 1926. While the total area was over 12 500 ha, most of the reserved land was Class "C". The beginnings of this Park are more adequately told, however, by Fernie & Fernie (1989).

The Nornalup Reserves Board was set up under the Parks and Reserves Act, on the December 5, 1924 and the national park at Nornalup Inlet was placed under its control. The Board consisted of the Under Secretary for Lands, the Surveyor General and the Conservator of Forests. On the October 27 1939 the Town Planning Commissioner was added to the Board. The Director of the Tourist Bureau became a member of the Board on the 22nd March 1946. Although Land Department records indicate very little activity by the Board in controlling and improving its reserves, by-laws were laid down by the Board to control the park. The Board was cancelled in 1947 and all its reserves were vested in the State Gardens Board. The members of the cancelled Board were already members of the State Gardens Board.

By the late 1920s a significant town had developed at nearby Pemberton, focused on timber milling and ser-

ving the district's farm settlers. This led to the formation of another board of management that became responsible for the "Pemberton National Parks". During 1928, moves were made by the Pemberton Parents and Citizens Association to have the hillside opposite the town on Big Brook reserved for scenic purposes. The Minister for Lands agreed and on May 16 the Pemberton National Parks Board was constituted under the *Parks and Reserves Act*. Comprising basically local people, the Board subsequently had the Warren and Beedelup National Parks and other reserves vested in it. Local Forest Department staff provided significant assistance with management of these Parks and the Board remained active until 1976, when it was dissolved and the "Pemberton National Parks" were transferred to the then newly-formed National Parks Authority (Australian Academy of Science 1962; Fernie & Fernie 1989).

Conservation reserves elsewhere in WA

A few flora reserves were created in the period up to 1929, but mainly to protect "novelties" like the Albany pitcher plant, boronia, and the red flowering gum. Large unvested National Parks were also created over the Stirling and Porongorup Ranges. However, of particular significance, an "A" Class flora and fauna reserve was gazetted over Barrow Island in the State's remote northwest in 1908, and in 1929 the Abrolhos Islands off Geraldton were declared a reserve for the "Protection of Flora, Public Recreation and Tourist Resort" and vested in a Board of Control (Australian Academy of Science 1962).

The period during and after the Great War saw an extensive expansion of the agricultural development in the wheatbelt, adjacent to the Darling Botanical District. This was aided by an extension of the railway network and a decline of employment opportunities in the goldfields. However, as more and more of the wheatbelt was being allocated for farming, little thought was given to creating strategic conservation reserves in that region. During the State's centenary year of 1929, the Government published a book in celebration, "A Story of a Hundred Years", with chapters on pertinent topics being written by specialists in those fields. Naturalist and noted wildflower artist, Emily Pelloe, contributed a chapter on the State's flora and made the following plea (Pelloe 1929);

The Eastern Wheat Belt sand-plains, for instance, sole habitat for hundreds of precious species, are fast becoming devastated without reserve in the interests of agriculture. It may be that in 2029, regret will be expressed that so little effort was made as far back as 1929 to ensure the preservation of the rare and beautiful flora. To deny future generations the right to enjoy its wonders is to deserve the censure of the unborn.

That little was done to set aside conservation reserves in the Wheatbelt even after 1929 was regretted by 1979, only fifty years later, as one of the World's most extensive land clearing programs was rapidly effected, rivaling current rainforest clearing in the Amazon basin. However, the extensive forest reserve system declared by 1929 had protected much of the adjoining Darling Botanical District from a similar fate.

The Next 40 Years (1930 - 1969)

Reserve management institutions

In 1933, various separate statutes and regulations dealing with land settlement and administration, including the *Permanent Reserves Act*, had been consolidated into a single *Land Act*. However, the *Parks and Reserves Act* remained separate.

A State Gardens Board had existed since 1920, controlling ten small park and garden reserves in and around the city of Perth. Other reserve management boards existing around 1930 which had also been established under the *Parks and Reserves Act* of 1895 were the Kings Park Board, Rottnest Island Control Board, Nornalup Reserves Board, Pemberton National Parks Board, and outside the Darling Botanical District the Abrolhos Islands Board of Control.

The State Gardens Board was seen by the State Government as an instrument in which to vest a variety of reserves with which nobody else was prepared to be burdened. For example, when the former Greenmount Road Board wished to relinquish its responsibility for the reserves comprising John Forrest National Park, they were vested in the State Gardens Board. The Board also progressively picked up small Darling Range reserves that had become popular weekend excursion and picnic sites, such as Serpentine Falls and along the Canning River in the Araluen area, and in 1947 reserves making up the Walpole - Nornalup National Park (Australian Academy of Science 1962).

It was not until 1956 that the State Gardens Board was transformed into the National Parks Board of Western Australia, still operating under the provisions of the *Parks and Reserves Act*. By this time, the Board also had the enormous Stirling Range National Park (created in 1913) and the Porongorup Range National Park (established in 1925) vested in it. However, while Yanchep "Park" and the large camping reserve at Hamelin Bay near Augusta came under the Board's control, the cave reserves in the Yallingup-Augusta area remained under the management of the State Hotels Department (Australian Academy of Science 1962).

Up to this time very little thought had been given by the State Government to protecting habitat for native fauna. Fauna protection was largely a matter of hunting control over particular species via Game Acts. For many years these had been administered by the Fisheries Department, while "vermin" regulations had been administered by agricultural-based agencies, including the former Rabbit Department, and local vermin boards. A significant change commenced with the passing of the *Native Fauna Protection Act* of 1950. Prior to this, in 1944 a Fauna Advisory Committee had been set up to advise the Minister responsible for administering the *Game Act* of 1912. Members of the Advisory Committee included the Chief Inspector of Fisheries, Curator of the Western Australian Museum, and Dr D L Serventy, then a fisheries research officer with the CSIRO and noted naturalist. Under the new Act, the Fauna Protection Advisory Committee became a corporate body in which wildlife reserves, created via the *Land Act*, could be vested (Australian Academy of Science 1962).

Thus, as Western Australia entered a new development phase stimulated by post-war reconstruction after World War II, there were three principal reserve management bodies seeking to protect forest land, flora and scenic landscape, and wildlife habitat. All were confronted by the competing demand for land for agricultural expansion. The members of the National Parks Board tended to have an interest in flora protection, so that new reserves with a flora emphasis tended to become national parks regardless of their landscape quality. Some so-called "National Parks" reserved in this period more closely fit the criteria of nature reserves. Reserves sought by the Fauna Advisory Committee (later to be renamed the WA Wildlife Authority, and its Act changed to the *Wildlife Conservation Act*) became nature reserves, even though some contained high value landscape.

Expansion of the conservation reserve and forest reserve estates

After 1929, expansion of State forest reservation tailed off in the 'timber belt' of Western Australia's south-west. Up to 1954 only about 100 000 ha more were added and most of this occurred in 1938. As happened in the period following the Great War, after World War II a conflict of interest again arose between demands for unallocated forested land to be released for post-war agricultural development. In 1953, at the suggestion of the Forests Department, an inter-departmental Land Utilisation Committee was set up by Cabinet to recommend on the allocation of remaining uncommitted forest land for forest conservation, water catchment protection, and agricultural development. This replaced a similar committee initially established in 1943 but which had generally been inactive (Forests Department 1969; Christensen 1992).

Largely as a result of the deliberations of the Land Utilisation Committee, up to 1958 a further 200 000 ha were added to State forest reserves in the south-west. Little consideration seems to have been given in this process to separately reserving some of the forest land as specific reserves for nature conservation. At the time (1957), the Forests Department was still producing educational material which explained its intention to convert virgin natural forest to a restructured production forest of rotational [tree] age classes, "ideal" for sustained commercial harvesting (Forests Department, 1966);

Managed and Unmanaged Forests

Possibly the idea of the cultivated forest is not entirely clear. One may ask just what advantages has a managed forest over a virgin forest if the latter is able to provide trees in perpetuity, maintain a stable composition and the soil fertility. It is not always realised that the virgin forest is not the most economical forest from man's point of view. Virgin forests have no normal succession of trees of all ages, but by virtue of their great age, usually contain a majority of over-mature trees. Such trees lose more wood by internal decay each year than they are capable of putting on in their condition of poor vigour. Their large crowns overtop and suppress young trees and prevent germination of seed on the forest floor.

Managed forests, on the other hand, aim to have the opti-

mum number of vigorously growing trees per acre. Once a tree slackens off in increment, it is removed to make way for more vigorous young ones coming on. All age classes of trees are represented in the forest so that as trees are cut for milling, others are available to produce a future final crop with a minimum lapse of time. Spacing between the trees is also controlled to permit an adequate area for growth of each member and the minimum of competition from neighbours. Managed Forests, therefore, are cultivated to produce the maximum amount of desirable produce while guaranteeing that there is always a crop ready to replace the one that is removed for utilisation".

In 1959, the inter-departmental Land Utilisation Committee was superseded by another inter-departmental committee established by Cabinet, the Crown Land Tribunal. Its task was to ascertain use allocation of "sparsely timbered" Crown land and in the ensuing decade the Tribunal's consideration of some 400 000 ha of Crown land resulted in the forest reserve estate being increased by only about 100 000 ha, much of which was coastal plain earmarked for conversion to pine plantation. Thus by 1969, State forests and timber reserves in the South West that were under Forests Department control totalled some 1.8 million ha, with additional extensive forest estate in the Eastern Goldfields (Forests Department 1969; Christensen 1992).

During the same period, relatively little improvement had been made to the conservation estate in the State's forested south-west, in adjoining agricultural regions and Wheatbelt, nor in the State generally. One redeeming feature was the creation in June 1930 of 18 timber reserves (under provisions of the Land Act) to protect mallet groves in the Great Southern area of the wheatbelt at the request of the Forests Department (former Forests Dept. file, now CALM file 011479 F3003 53). These totalled some 130 000 ha, much of which was later converted into nature reserves, such as Lake Magenta and Dragon Rocks Nature Reserves. Nature conservation-oriented groups, like the Royal Australian Ornithologists Union (RAOU) and the Western Australian Naturalists Club, continually lobbied the State Government over the years to retain strategic bushland habitats in areas being opened up for farming. This tended to increase in the 1950s, following the end of World War II, with even the Country Women's Association of WA also making pleas, along with newer conservation groups like the Tree Society and WA Branch of the Society for Growing Australian Plants, now the Wildflower Society of Western Australia (Dept. Lands and Survey File 2507/93, Vol. 4).

On the whole, the coverage of conservation reserves across Australia was poor and not systematic. As a consequence, in 1958 the Australian Academy of Science appointed a Committee on National Parks and Reserves to inquire into the situation. The committee included Dr W D L Ride, then Director of the Western Australian Museum. In turn, the Academy of Science committee itself formed State sub-committees, and the WA Sub-committee on National Parks and Nature Reserves was chaired by Dr Ride, producing a report to the Academy in 1962 on conservation reserve proposals. A very

limited number of copies of the WA Sub-committee report had been produced and, at the instigation of the Royal Society of Western Australia, the National Parks Board collaborated with the Australian Academy of Science and published an edited version (in 1965) for popular use. Now that the Academy of Science sub-committee's proposals for new conservation reserves in the State was publicly available, there was strong community support for their implementation by the State Government Annual Report of WA Dept. Lands & Survey, WA National Parks Board, 1966; (Australian Academy of Science 1962, 1968; Conservation Through Reserves Committee 1974; Ride 1975).

In 1969, the WA Cabinet established another inter-departmental committee, the Reserves Advisory Council, to recommend on the Sub-committee's conservation reserve proposals and other similar proposals from a variety of sources that had been put forward for the establishment of conservation reserves. While a number of the Reserve Advisory Committee's recommendations were adopted by Cabinet, a backlog began to develop over proposals where there was opposition from mining interests. A culmination of this deteriorating situation occurred later in 1969 after the Hamersley Range National Park (now Karijini National Park), proposed by the Academy of Science WA Sub-committee, was created on the recommendation of the Reserves Advisory Council. Reservation of this extensive (630 000 ha) Park apparently by-passed a Mines Department vetting process and received Cabinet approval in the face of a number of iron ore development agreements covering the area. The Reserves Advisory Council then ceased to meet because outstanding recommendations remained unapproved (Annual Reports of WA Dept. Lands and Survey and WA National Parks Board, 1969, 1970; Conservation Through Reserves Committee 1974; Ride 1975).

While the conservation reserve estate in the forested south-west had not substantially increased up to 1969, a number of conservation reserves had been set aside in the northern part of the Darling Botanical District. This occurred as new land for agricultural expansion was being made into sandplain areas, following success with trace-element fertilisers. The allocation of conservation reserves in these more recent times was a reflection of Government response to changing community attitudes. These were outside of the main forest belt and largely comprised sandplain (kwongan) vegetation, and included the Moore River National Park. Elsewhere in the State, the Government Botanist, C A Gardiner, had been successful in persuading the State Government to create a series of large strategic nature reserves along the South West and Ereman Botanical Provinces interface. These comprise today's Kalbarri and Cape Arid National Parks and Jilbadji Nature Reserve, and were gazetted in 1954. Gardiner was also successful in having the Fitzgerald River National Park set aside at the same time, initially as a nature reserve (Australian Academy of Science 1962; Ride 1975).

As the State Government had apparently refused to consider any further significant conservation reserve proposals, this helped stimulate the initiation of a public campaign by the Conservation Council of Western Australia in 1969.

A Modern Reserve System (1970 - 1995)

Environmental Protection Authority and its Conservation Through Reserves Committee

The influence of the "Conservation Campaign" mounted by the infant Conservation Council in 1970 is often overlooked as one of the stimuli to government action in that era. Formed in 1967 by a consortium of the main conservation groups existing in Western Australia at the time (including the Tree Society, Western Australian Naturalists Club, Kings Park and Swan River Society), the Council initially acted as clearing house for information and a means of co-ordinating group activities where there was a common interest. These ranged from opposing inappropriate development plans for Kings Park, opposing mining proposals in numerous conservation areas (such as Jilbadji Nature Reserve) through the Mining Wardens Court, and promoting expansion of the State's conservation reserve system.

Matters came to a head in 1969 when serious industrial pollution was manifesting itself in Cockburn Sound and other coastal areas; with continued mining threats to key conservation reserves, culminating in bauxite mining in State forest and mineral sand pegging in popular resort areas around Geographe Bay to Augusta; and State Government disinclination to consider any more proposals for conservation reserves. At the time, the State Government was also promoting its "million acres a year" farmland release scheme involving virgin bushland in the Wheatbelt.

This stimulated the formation of more groups that were fighting local issues; even established Progress Associations and the Farmers Union were becoming involved in opposing some industrial development and mining proposals. Many more groups became affiliated with the Conservation Council and in 1969 it began planning a campaign. The campaign focused on three basic actions, wide promotion of a Conservation 'Bill of Rights' outlining the Council's view of Government action that was needed, the gathering of a massive petition for presentation to Parliament, and an organised torchlight parade on Parliament after it opened for its last session before the 1971 Parliamentary election (Churchward 1991).

Amongst the 'Bill of Rights' requests were the formation of a Ministry of Conservation, creation of another 8 million ha of conservation reserves in the State, and a reform of mining legislation applicable to conservation areas. Public and media support for the campaign was high and the government of the day responded with an inquiry into the 1904 Mining Act being conducted and the slow but eventual great improvement for the protection of conservation areas, as well as initial environmental protection legislation. However, the legislation was not formally proclaimed prior to the 1971 Parliamentary election and the incoming Tonkin Government initiated stronger legislation and the creation of an Environmental Protection Authority (EPA). In turn, the Authority immediately set in train a project to promote the establishment of a State-wide conservation reserve system. The latter commenced in 1972 and coincided with growing public concern over native forest management as the concept of clear-felling forest areas for an export

woodchip industry was being planned in several States, including Western Australia.

At its first meeting after being established in 1971, the EPA set up a Conservation Through Reserves Committee (CTRC) to examine Western Australia's existing conservation reserve system and to report to the EPA on proposals to significantly expand it. Dr W D L Ride was appointed Chairman. In its work, the CTRC was assisted by a Technical Sub-committee of specialists in the fields of demography, zoology, botany and geology, and by an executive officer. The latter group were seconded from government departments to work full-time on the project (Annual Reports of the WA Environmental Protection Authority, 1972, 1973; Conservation Through Reserves Committee 1974; Ride 1975).

The CTRC divided the State into 12 fairly homogeneous regions, or "Systems", and began producing reports on them for public comment and EPA consideration, the first being released in 1974 and the last in 1981 (the so-called "Green Books"). In turn, the EPA issued its own reports (the so-called "Red Books") with recommendations to the State Government for new reserves and the expansion of some existing ones in the various Systems. Within this project, the Darling Botanical District is basically covered by Systems 1, 2 and 6. In these regions some public land was still available to extend the reserve system but the majority of the uncleared land had already been included in State forest reserves (Ride 1975; Mulcahy 1991; O'Brien 1991; Christensen 1992).

The major new conservation reserves created in the Darling Botanical District through the CTRC process were the adjoining D'Entrecasteaux and Shannon National Parks in System 2. Both were extremely controversial with the former being initiated by local Forests Department staff and vigorously opposed by various land development interests, and the latter being initiated by the CTRC itself and vigorously opposed by the Forests Department and other agencies. However, the Forests Department did support conservation priority management of some parts of the Shannon Basin. The other major controversial CTRC proposal was in System 1, involving the connection of the discontinuous Leeuwin-Naturaliste National Park (based on the original cave reserves once managed by the 'old' Caves Board) through the addition of other miscellaneous reserves and private land purchases. Because of several contentious issues, the EPA arranged for a special inter-departmental committee to review the CTRC proposals within Systems 1 and 2 and its report (the "Brown Book") was considered by the EPA in conjunction with the CTRC proposals before making recommendations to the State Government. While the EPA did not support the original Shannon "Basin" national park proposal, various conservation groups maintained a continuous campaign for the concept and were successful a decade later in having the area excised from State forest and converted into a national park (Department of Conservation and Land Management 1987a; Mulcahy *et al.* 1988; Thomas 1988; O'Brien 1991; Christensen 1992).

Elsewhere in existing State forest areas, the CTRC and EPA basically supported Forests Department plans to have identified high nature conservation and recreation areas retained as forest reserve under Forests Depart-

ment management but with priority for those uses. However, the Conservation Council campaigned for a jarrah forest conservation reserve in the Nanga area near Dwellingup (System 6) to be taken out of State forest and managed separately (Conservation Council 1980; Mulcahy *et al.* 1988; Department of Conservation and Land Management 1990; Christensen 1992). To some extent, this was seen as a means of redressing the loss of the nearby original "South Dandalup" nature reserve in 1911 to forest production interests. The State Government eventually agreed to this proposal as well, and today's Lane Poole Reserve is the result. System 6 as a whole was the most complex of the CTRC regions because it included most of the State's population and fewer opportunities to significantly increase the conservation reserve estate. However, out of a number of the proposals involving the Swan Coastal Plain came the concepts of urban bushland protection and regional park focuses which would later be used to channel community and government efforts to put protective measures in place (Environmental Protection Authority 1983; Mulcahy 1991).

Reviewing national park management

During the 1971-1973 Labor government under Premier John Tonkin, there was significant change in State Government policy toward environmental protection. The *Environmental Protection Act* and the EPA (along with the EPA's 'conservation through reserves' project) became established. Toward the end of its term, the Labor government also examined the operation of the former National Parks Board with a view to improving its structure and management capability. Basically, three options were canvassed;

- transferring national park management to an existing and better resourced Forests Department (the "Queensland model"),
- amalgamating the wildlife management division of the existing Department of Fisheries and Wildlife with the National Parks Board, to provide a National Park and Wildlife Service with an expanded conservation management role (the "NSW model"), and
- converting the existing "Board" into an Authority operating under its own Act with improved funding and staff resources, and a professional Director.

The abysmal national park allocation in Queensland and growing controversy over forest management in Western Australia mitigated against the first option. While there was community support for establishing a National Parks and Wildlife Service similar to the service then recently established in NSW, it was opposed at bureaucratic levels. Key officials associated with the National Parks Board and senior staff in the Department of Fisheries and Wildlife associated with wildlife management argued against an amalgamation. An incoming conservative coalition government, under Premier Sir Charles Court, subsequently drafted legislation for a new National Parks Authority, which came into being in 1976. While the new Western Australian Government maintained a programme of improved environmental management, controversy continued over its adoption

of the EPA recommendation that the Shannon basin remain reserved as State forest, and there was strong opposition to the proposed D'Entrecasteaux National Park which would "lock up" potential farmland in areas such as the Pingerup Plains.

In 1979 and 1980 the Legislative Council agreed to the appointment of Select Committees to inquire into, and report on national parks in Western Australia. Both were prompted and chaired by the Hon Sandy Lewis MLC, Member for the South West Province. The scope of the 1979 proposal was all-embracing with an impossible two-month deadline for tabling a report. The resultant eight-page report, without conclusions or recommendations, did little justice to the time and effort of the many people who made written submissions or appeared before the Select Committee (Select Committee 1979).

The second attempt was more successful and resulted in a report exceeding 150 pages. However, this time many of the people who participated in the 1979 inquiry didn't participate in the second inquiry. Community participation in the second Select Committee inquiry is also remarkable for the amount of interest shown by local governments and regional development organisations which were pro-land development, and deeply concerned over EPA proposals for expanding the State's conservation reserve system (Select Committee 1981). Very little became of this Parliamentary committee report. However, while the concept of a National Parks and Wildlife Service was supported, so was a nature conservation precinct concept which allowed resource utilisation. It is clear that the idea was based on the English-style "National Park" (where landscape conservation is imposed on utilised rural land), but in reverse where development could be permitted in what started out as fairly pristine land, such as the Pingerup Plains area of the D'Entrecasteaux National Park (personal communication with the Select Committee).

Forest management priority areas

The period 1975 to 1987 was one of great controversy over forest management and forest reserve issues. Close questioning in Parliament by the opposition Member for Warren, the Hon David Evans MLA, had revealed the extent of forest resource over-cutting that had been allowed for some time (WA Parliament, Legislative Assembly questions on notice No. 19 17/10/1974, and No. 67 28/11/1974), while the Forests Department was still promoting the concept of "sustained yield" in its educational material (Forests Department 1971);

A well-managed forest may be likened to a bank account in which the forest itself and the forest soil represent the capital invested and held in trust, while the annual growth in timber (the increment of the forest) represents the interest earned. The fundamental idea of Forest Management is to harvest this increment only, and to preserve and improve the forest capital for increased future production.

It was probably with the State's first woodchip proposal in 1973, from the Forests Department itself, that the full significance dawned on the interested community of the long-term change to forest structure that was proposed. Essentially, the concept of natural forest conversion to "ideal" or so-called "normal" forest involved restructuring to a regular succession of all age classes to

provide regular timber crops of young trees (around 100 years old, with even younger "thinnings") in perpetuity. To do this conversion on a large scale in the mixed karri-marri forest included extensive felling of marri trees to waste, and therefore without recovery of expensive felling costs. However, marketing marri woodchips for export as a feedstock for paper making would make clear-felling and subsequent forest conversion economical (Annual Reports of the Environmental Protection Authority 1973, 1974; Forests Department 1973). While publicity over the past two decades has tended to focus on the concept of extensive clear-felling as a silvicultural practice, this is just a means to an end, being the conversion of a natural forest ecosystem to a manipulated tree crop system, in which the long-term environmental implications still remain unclear.

On top of the Shannon basin and woodchip issues, the Forest Department created another controversy with the proposal to re-afforest *Phytophthora*-dieback affected native forest with pines in the Donnybrook Sunklands (Blackwood Plateau), between Nannup and Margaret River. The statement of intent, issued in September 1975, proposed a program to convert some 60 000 ha of jarrah forest, considered to be of poor quality for timber utilisation, to pine plantations over a 30 year period (Forests Department 1975). However, like the Shannon basin issue, the matter was determined by commitments in the State Platform of the Australian Labor Party, and the program was discontinued when the Burke Labor Government came into office in 1983.

Faced with growing community concern and pressure within its own ranks (R Underwood, personal communication), and a realisation also that multiple-use forest management needed to be a significant feature of its operations, the Forests Department embarked upon a system of identifying forest blocks having a variety of appropriate priorities for management (Mulcahy *et al.* 1988; Christensen 1992). Termed management priority areas (MPA), the concept first appeared in General Working Plan number 86 in 1977. It was also promoted in issues of the Department's publicity journal, *Forest Focus* (No. 18, August 1977; No. 22, January 1980) as part of its new zoning policy for forest management. The key MPAs in a conservation sense were those identified as having wildlife or recreation priorities. The MPA concept also generally comprised a core/outer buffer system, and identified MPAs were well established when the CTRC/EPA System 6 study was underway in late 1970s/early 1980s. While the EPA's 1983 recommendations for System 6 (Environmental Protection Authority 1983) supported the MPA concept and that such areas remain under Forests Department management, the Authority also recommended that legislation be provided to make the priority purpose secure and that any change from conservation or recreation require Parliamentary endorsement. It also advocated that management plans for conservation MPAs be prepared and made public as soon as practicable. These proposals were aimed at maintaining security of purpose for forest conservation areas that remained under Forests Department management.

There was still community concern that forest conservation areas identified by the Forests Department were inadequate in extent and would remain insecure in

terms of management while still vested in the Department. Further change was to come within a couple of years after the Forests Department was merged with other agencies following promulgation of the *Conservation and Land Management Act* in 1984.

The Conservation and Land Management Act

One of the first actions of the incoming Burke Government in 1983 was to have land resource management in the State's south-west reviewed, because of continuing controversies over the use of forest and coastal land. The mechanism created for this was the appointment of a Land Resource Management Task Force. In an interim report, the Task Force sought and was granted an extension of its terms of reference to take in the whole of Western Australia. The principal outcome of the final report of the Task Force, in January 1984, was the amalgamation of the Forests Department, National Parks Authority and the wildlife component of the Department of Fisheries and Wildlife to form a new department to manage State forest and timber reserves, national parks and nature reserves, and wildlife generally. At the same time, it advocated that separate advisory bodies for forestry and nature conservation be established to assist the Minister, and that a higher level "Policy Commission" be created above the Department (Task Force 1984).

The structure eventually adopted by the Government was that of an amalgamated department, with three advisory bodies (referred to as 'controlling bodies' in the Act); Lands and Forests Commission (LFC), Timber Production Council (TPC), and National Parks and Nature Conservation Authority (NPNCA).

The concept was strongly opposed by conservation groups generally (as well as local government and other sectors of the community), who would have preferred a simpler amalgamation to form a National Parks and Wildlife Service similar to the NSW model. As a compromise, the Government provided a more pro-active role for both the LFC and NPNCA, with forest and conservation reserves being vested in each, respectively, (rather than in the Department), and that these two "controlling bodies" be responsible for management plan production and monitor the Department's implementation of management plans approved by the Minister, and policy formulation. This structure was put in place in 1985 after the passing of the 1984 *Conservation and Land Management Act*, with the amalgamated department becoming the Department of Conservation and Land Management (CALM). A feature of the new department was a decentralising of administration through the establishment of regional and district offices throughout the State. At the same time, the *Wildlife Conservation Act* was modified to relate to wildlife management generally, and nature reserve provisions were transferred to the *Conservation and Land Management Act*.

In 1987 the former Forests Department's Forest Working Plan No 87 was due to expire. CALM, in conjunction with the LFC and NPNCA, set about replacing it with three separate region management plans into which the main State forest areas fell, - CALM's Northern (now Swan), Central and Southern Forest Regions. Draft region management plans were issued for public comment and extended the forest conservation/recreation MPA system. It also proposed that the purposes of MPAs be

given Parliamentary security through amendment of legislation. However, from within the Labor Party, the Government was persuaded to promote conversion of conservation/recreation MPAs to national parks, conservation parks or nature reserves and have them vested in the NPNCA rather than remain as "zones" within State forest still vested in the LFC (Department of Conservation and Land Management 1987b, 1987c, 1987d; Mulcahy *et al.* 1988; Shea & Underwood 1990; Underwood 1991; Christensen 1992).

The approved 1987 Forest Region Management Plans therefore set in train the transfer of over 500 000 ha from forest reserves to conservation reserves. Subsequent amendments to these three region management plans (Department of Conservation and Land Management 1994) increased this transfer proposal by a further 50 000 ha approximately. The mechanics of the transfers are administratively complex and the proposals are being progressively implemented. Under provisions of the *Conservation and Land Management Act* both the NPNCA and LFC are obliged to monitor the implementation of formal management plans. However, to date (1995) no status report has been publicly released. During the period 1989-1993, the EPA maintained a stance that State forest retained for timber production should also be managed to maintain its wildlife habitat values, and advocated the establishment of forest research and monitoring overview mechanisms. In 1994, the State Government adopted as policy the ecological sustainability of timber production from native forests reserved as State forest (Department of Conservation and Land Management 1994).

Conclusion

In the "design" of conservation reserves, the selection of many of the early reserve sites was a matter of someone's personal fancy but usually focused on an outstanding resource-base. For example, Kings Park (1872) provides panoramic vistas across Perth and Melville Waters; Beedelup and Warren National Parks (1901) contain truly "noble" karri trees, and appealing riparian landscape; the same can be said of John Forrest (1895) and Serpentine National Parks. However, there was more science and "system" to the selection of the former "South Dandalup" nature reserve (1894) and the original cave reserves that formed the nucleus of today's Leeuwin-Naturaliste National Park (1902).

It was another fifty years or so after the initial creation of conservation reserves around the turn of the century, however, before science and "system" were applied to reserve selection in Western Australia. The first were the strategic botanical province interface reserves promoted by Charles Gardiner in the early 1950s, and resulting in today's Kalbarri and Cape Arid National Parks and some other areas. While the Australian Academy of Science began raising community interest in the need for a systematic approach to conservation reserve selection, the eventual result in Western Australia was the EPA's more extensive decade-long 'Conservation Through Reserves' program. Reserve selection in that process was dependent upon constraints such as the availability of uncleared land, other competing utilisation interests (*e.g.* mineral development) and local

community attitudes. Thus, boundary outcomes were influenced by politics and compromise.

By the time the EPA's Conservation Through Reserves Committee had completed its first major assessment of over two-thirds of the State (Conservation Through Reserves Committee 1974), the Academy of Science had produced a further report, outlining the need to preserve genetic diversity, along with other concepts relating to reserve "design" (Australian Academy of Science 1975). This was supplemented by the "Specht Report" (Specht *et al.* 1974) concerning the conservation of major Australian plant communities. However, while these were able to have some influence on new conservation reserve proposals for Swan Coastal Plain areas in the EPA's subsequent System 6 study, many of the "regional park" proposals were based on landscape/recreation potentials identified through early (1950s/1960s) town planning concepts. Nevertheless, both reports influenced the Forests Department in its selection of conservation MPAs within State forest reserves (Mulcahy *et al.* 1988; Christensen 1992).

Through several processes, the conservation reserve situation within the Darling Botanical District is under review and doubtless will be subjected to further fine-tuning. Currently there is a heavy focus on the concept of 'urban bush' conservation and regional parks, and the situation was adequately summed up by the EPA (1991):

There is much unfinished business in implementation of conservation through reserves. We have done as well as possible for late starters in agricultural areas, we are doing better than before in forest areas, but continue to lag in pastoral areas, and have reached about halfway in implementation in urban and near urban areas.

In 1996 the EPA is scheduled to review aspects of CALM's management of State forest, including forest research and monitoring issues. The content of the Authority's report and its conclusions may indicate if the objectives of multiple-use management are being met satisfactorily or not.

1995 has been taken as the centenary year for Kings Park, as it was 100 years ago that the serious business of management commenced with the appointment of its management board. However, it has taken 100 years for the production of a formal management plan for this Park, effectively the State's first regional park. The story of urban bushland protection and regional park establishment and management is one with a "town" planning focus and of long-term indecision. However, some key decisions appear about to be made by the present State Government on urban bushland policy and regional park administration. Compiling a history on this topic requires branching into the realms of town and strategic planning, and is a story in its own right. It is a task best left for a little while longer, until State Government direction becomes clearer.

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Assessing the conservation reserve system in the Jarrah Forest Bioregion

N L McKenzie¹, S D Hopper², G Wardell-Johnson^{1,3} & N Gibson¹

¹ Science and Information Division, Department of Conservation and Land Management, P O Box 51, Wanneroo WA 6065; ² Kings Park and Botanic Gardens, Fraser Avenue, West Perth WA 6005; ³ present address: Department of Biology, University of Namibia, Private Bag 13301, Windhoek Namibia

Abstract

Recent reviews have assessed the comprehensiveness of the conservation reserve system over the northern part of the Jarrah Forest Bioregion in terms of vegetation complexes. The complexes were distinguished in terms of geomorphology and dominant vegetation. The least reserved complexes are those of the Darling Scarp, Blackwood Plateau, Collie Coalfields and those with agriculturally desirable soils.

Available maps can be used to estimate the reserved area of each of the Bioregion's vegetation complexes or geomorphic units, but there are not enough data on patterns in biodiversity to assess other facets of its adequacy, even in the northern part of the region. A quadrat-based regional survey is necessary if the representativeness of the area's reserve system is to be assessed from an ecosystem perspective. The sampling would need to cover a range of the different components of the biota (perennial floristics, vertebrates and selected invertebrate taxa). Such surveys are time-consuming and expensive. Current studies of rare, restricted and endemic species, of weed, feral animal and pathogen impacts, and of forest management effects, need to continue in parallel.

A recent national assessment of the major gaps in Australia's conservation reserve network suggests that other Western Australian regions have higher priority for regional survey than the Jarrah Forest Bioregion. Seventeen of the State's 26 bioregions have a smaller proportion of their area reserved than the Jarrah Forest, and of these, 11 have a more biased reserve system. Should we commit scarce survey resources to the Jarrah Forest Bioregion?

Introduction

The high rainfall part of south-western Australia is covered by the Darling Botanical District (Beard 1982). This district is made up of the Swan Coastal Plain (Drummond Botanical Sub-district), the northern jarrah forest (Dale Sub-district), the southern jarrah forest (Menzies Sub-district) and the karri forest (Warren Sub-district).

We provide a brief review of the data that are available to assess the coverage of the existing conservation reserve system for the communities indigenous to the Dale and Menzies Sub-districts. Together, these two sub-districts form the Jarrah Forest Bioregion (Thackway and Cresswell 1995). We then describe and discuss previous assessments of the reserve system in this area.

Current knowledge

Beside bioclimatic surface models (Nix & Gillison 1985), various environmental maps at 1:250,000 scale cover all or most of the bioregion;

- surface lithology (Wilke & Low 1978, 1980; Wilke & Walker 1982, 1984),
- landforms and soils (Churchward & McArthur 1980; Churchward *et al.* 1988; Tille & Lantzeke 1990; Churchward 1992). The 1:250 000 coverage

is 90% complete whereas the 1:100 000 coverage is about 50% complete; R Harper, *pers. comm.*), and

- vegetation structure (Beard 1982; Heddle, Loneragan & Havel 1980).

At such scales, considerable heterogeneity is averaged within each map-unit.

There are also 1:25 000 Aerial Photographic Interpretation (API) maps of tree-canopy floristics, mapped at 1:15 800 and ground-truthed along tracks and roads (F J Bradshaw *et al.*, unpublished). They were produced by the Forests Department during the 1950s and 1960s, and cover virtually all the forested parts of the Bioregion except;

- parts of the far northern end (north of 31° 45' S, although Julimar State Forest was mapped), although the mapping has recently been extended,
- most of the eastern edge between 32° 00' S and 34° 30' S, although some parts, such as Dryandra State Forest, are covered by 1:15 800 scale "Mallet Classification" vegetation maps made during the 1930s, and
- the far south-eastern corner, east of 117° 40' E.

Most of the areas not covered at this scale are reserved for nature conservation and mapped at an equivalent scale, or are private land that is extensively cleared.

The mesic bioregions of south-western Australia are remote from their eastern Australian counterparts, being isolated by 2000 km of the semi-arid and arid environ-

ments that comprise districts such as the Nullarbor and the Great Victoria Desert. They contain many endemic species that are relicts from previously wetter and less seasonal climatic periods. Examples from the Jarrah Forest Bioregion include the frogs *Geocrinia alba* and *G. vitellina*, and the eucalypts Yarri (*Eucalyptus patens*), *E. relictua* and *E. virginia* (Wardell-Johnston *et al.* in press). Their vegetation and floristics have been reviewed by Havel (1975, 1989), Wardell-Johnson *et al.* (1996) and Wardell-Johnson & Horwitz (1996), and the rare flora by Kelly *et al.* (1990), while knowledge of the fauna has been reviewed by Wardell-Johnson & Nichols (1991), Abbott & Christensen (1994) and Wardell-Johnson & Horwitz (1996).

Several factors, including the isolation, the small area and previous climate changes, have lowered diversity in the larger indigenous vertebrates of the south-western forests, but the invertebrates and small vertebrates are rich in species (Wardell-Johnson & Horwitz, 1996). *In situ* speciation is real in the south-west, for the fauna as well as the flora; Havel and others have demonstrated a rich mosaic of landforms, soils and floristic variation in the jarrah forest despite the area's great structural homogeneity in vegetation, and Wardell-Johnson & Roberts (1993) concluded that the rich but fine-scale variation in soil and landscape properties maintains barriers between closely related frog species. A recently discovered frog, endemic to the Bioregion, is the most geographically restricted frog known from mainland Australia (Roberts *et al.*, 1997).

It is clear that many scales should be considered in any discussion of conservation in the Jarrah Forest Bioregion. However, coordinated work on the distribution and biology of the naturally rare and of the restricted and endemic flora of the Bioregion has commenced only in the last decade, and most studies have focused on the central and northern parts of the bioregion. Systematically-gathered data are still too fragmentary to reveal their general patterns of occurrence.

Autecological studies of fauna have concentrated on vulnerable species, especially mammals that have become either extinct or rare outside the forests, woodlands and shrublands of the Darling District since European settlement (e.g. *Dasyurus geoffroii*, *Myrmecobius fasciatus*, *Bettongia penicillata*, *Macropus eugenii* and *Pseudocheirus occidentalis*; Burbidge & McKenzie 1989). The numbat study reported by Friend & Thomas (1995) is a good example. The first three species are now the subject of detailed management programs (e.g. Orell & Morris 1994; Start *et al.* 1995). Considerable research has also been carried out on *Macropus eugenii*, *Pseudocheirus occidentalis* and *Isoodon obesulus* (e.g. P de Torres, *pers. comm.*) Detailed information has also been collected on the distribution and habitat requirements of some rare frogs (e.g. *Geocrinia alba* and *G. vitellina*), reptiles (e.g. *Ctenotus delli*) and birds (e.g. *Atrichornis clamosus*). While the critical requirements of some vulnerable vertebrates are still unknown (e.g. *Macropus irma* and *Setonix brachyurus*), research programs are now in-place. Recovery plans are now being implemented for others such as *Geocrinia alba* (Driscoll *et al.* 1995).

Most research on the disturbance ecology of flora and fauna in the Darling District has been directed to mining

and rehabilitation, logging and regeneration, fire, plant disease and the introduced fox *Vulpes vulpes* (Wardell-Johnson & Nichols 1991; George *et al.* 1995; Abbott & Christensen 1996). Rehabilitation following bauxite mining has been studied in considerable detail (e.g. Nichols & Bamford 1985; Nichols & Watkins 1984; Majer 1990; Majer & Nichols, unpublished observations), as have the dynamics and management of dieback disease caused by *Phytophthora cinnamomi* in the jarrah forest (Shearer & Tippet 1989). Integrated studies have recently been commenced that will allow predictive-modelling of fauna responses following logging and burning in the jarrah forest (Wardell-Johnson & Nichols 1991; Friend 1993; K Morris, *pers. comm.*). Other studies are being undertaken to examine the occurrence of tree hollows in the forest and to determine the impact of timber harvesting on the availability of these hollows (Faunt 1992; Rhind 1996; K Whitford, *pers. comm.*). Clearing for agriculture (Beard & Sprenger 1984), exotic animals such as foxes (Kinnear 1993; Morris 1993; Friend *et al.* 1994), introduced weeds (Pigott & Gray 1993; Burke unpublished), and plant diseases such as those caused by species of *Phytophthora*, pose the greatest threats to the plant and animal communities of the Jarrah Forest Bioregion.

According to Burbidge & McKenzie (1989) faunal changes have not been as dramatic in the Darling Botanical District as in the pastoral and agricultural zones. Seven mammals, fifteen birds, two reptiles and three frogs from this district are currently gazetted as "fauna which is likely to become extinct or is rare". Unfortunately, data on their distribution within the Jarrah Forest Bioregion at the time of European settlement are scant, vague and localised; even the sub-fossil record is fragmentary (A Baynes, *pers. comm.*). While some of these species were apparently rare or had restricted ranges in the bioregion originally, available records indicate that the ranges of most have contracted and/or become fragmented (e.g. *Bettongia penicillata*, *Setonix brachyurus*, *Macropus eugenii*, *Dasyurus geoffroii*, *Myrmecobius fasciatus*, *Pseudocheirus occidentalis*, *Trichosurus vulpecula*, *Leipoa ocellata*, *Dupetor flavicollis* and *Ninox connivens*). Wardell-Johnson & Nichols (1991) suggested that species with specialised habitat requirements and low dispersal abilities were the first to decline (e.g. *Macropus eugenii* and *Geocrinia alba*). Other species persist within the bioregion only at Two Peoples Bay (the bioregion's south-eastern margin), although they were recorded elsewhere in its southern parts earlier this century (*Potorous tridactylus*, *Psophodes nigrogularis*, *Dasyornis longirostris* and *Atrichornis clamosus*). The Western Bristlebird (*Dasyornis longirostris*) and Western Whipbird (*Psophodes nigrogularis*) also occur in the Esperance Plains Bioregion to the east.

The only likely mammalian extinctions have involved species of adjacent bioregions with ranges that extended into the periphery of the Jarrah Forest Bioregion; *Potorous platyops* and *P. tridactylus* on the bioregion's south-eastern periphery, and *Macrotis lagotis* and *Bettongia lesueur* along its eastern periphery. Leeuwin's Rail (*Rallus pectoralis*) is the only bird thought to have vanished from the Bioregion; it was only known from peripheral southern areas.

In explaining why the forested bioregions of the south-west have maintained more of their conservation

values than the arid and semi-arid areas of Western Australia, the resilience of the forest is frequently cited (e.g. Underwood *et al.* 1991). This should not lead to complacency for there has been a rapid intensification of land-use demands in the Jarrah Forest Bioregion since the 1960s (Havel 1989). The end-results of more intensive use, including extensive clearing and urbanisation, have been documented in the adjacent Swan Coastal Plain (Drummond Sub-district), where 13 bird species declined in abundance in Kings Park between 1927 and 1988 (Recher & Serventy 1991), and at least 8 mammals are known to have become extinct (*Bettongia lesueur*, *B. penicillata*, *Macropus eugenii*, *Rattus tunneyi*, *Pseudomys fieldi*, *P. shortridgei* and *Notomys mitchelli*; Kitchener *et al.* 1978, and Western Australian Museum records).

In overview, many specialist projects have been carried out in the Darling Botanical District, but no attempt has yet been made to define the pattern of any group of biota (e.g. the plants or the vertebrates) throughout any of its four sub-districts. The most extensive quantitative studies so far have been of the vascular plants in the southern and central Drummond Sub-district (Gibson *et al.* 1994) and in the Tingle Mosaic (which overlaps with parts of the Warren and Jarrah Forest Bioregions;

Wardell-Johnson *et al.* 1996), and of the wetland fauna of the Southern Forest Region (Horwitz 1994). Otherwise, current knowledge is summarised by the "Jarrah Book" (Dell *et al.* 1989) for the Dale Sub-district and by Wardell-Johnson & Nichols (1991) for parts of the Menzies and Warren Sub-districts. There is also considerable site-specific data for some localities such as the Worsley alumina leases of the eastern jarrah (Anon 1985) and of the alternative water supply sites (Anon 1987). Existing information is sufficient to demonstrate areas of high mammal richness such as the proposed Perup Nature Reserve (Anon 1987a), and some sites of high endemism, but does not allow an explicit understanding of the overall patterns of the biota across the study area.

Reserve system assessments

Existing network. The existing conservation reserve system, developed through the work of Havel (1975), is described by Anon (1987b) and Heddle *et al.* (1980). It comprises National Parks, Nature Reserves and "conservation parks". In previous reviews of the forest reserve system, some of the "conservation parks" were Management Priority Areas (MPAs), but were treated as conservation reserves because the relevant lands are to be



Figure 1. The Jarrah Forest Bioregion showing subdistrict boundaries and Havel's "northern jarrah forest".

vested in the National Parks and Nature Conservation Authority. Subsequently, these MPAs were enlarged and inter-connected as a series of "proposed Conservation Parks".

The formal "Conservation Park" legislation is now in place, so the proposals that have been gazetted (virtually all) are conservation reserves for the purposes of this review. We have also included Lane Poole Reserve, which was declared in 1987 under Section 5g of the *Conservation and Land Management Act*. It should be noted that both the Conservation Parks and "5g" reserves in this region retain the optional purpose of bauxite mining.

Figure 1 shows the Jarrah Forest Bioregion, with the "northern jarrah forest" cross-hatched to show the area that Havel assessed (modified from Havel 1989, and as mapped on page 394 of Dell *et al.* 1989).

Land-classes. Heddle *et al.* (1980) integrated available climatic, floristic, geomorphic and vegetation structural data to produce a set of three maps showing vegetation complexes at a scale of 1:250 000. Havel (1989) concluded that maps such as these "... are, in fact, the only basis on which adequacy of coverage [by the conservation reserve system in the forested regions of south-western Australia] can be assessed at present". Wardell-Johnson & Nichols (1991) reached a similar conclusion.

Given this basis, the comprehensiveness of the reserve system was assessed as early as 1980 (Heddle *et al.* 1980). Havel (1989) reviewed and updated this analysis (Table

Table 1

Percent of the total area of the northern jarrah forest's vegetation complexes that are within reserves (from Havel 1989 and Anon 1994)¹. Neither list of percentages corresponds exactly to the Jarrah Forest Bioregion (see Fig 1)².

Vegetation Complex	% Representation in reserves (Havel 1989)	% Representation including new reserve proposals (Anon 1994)
Helena (L/M)	—	25.5
Williams	—	0.9
Lowden	0.2	5.8
Darling Scarp	1.5	3.8
Michibin	3.5	9.0
Wilga	3.8	13.4
Muja	4.3	3.0
Cardiff	—	—
Coolakin (L)	7.5	17.4
Dwellingup (H)	6.0	6.5
Yarragil (M/S)	5.7	6.7
Murray (L/M)	8.7	10.6
Murray (M/H)	8.9	18.1

¹ In the National Forest Policy terminology (NFPS 1992), this assessment relates to the reserve system's "comprehensiveness" and, in part, its "adequacy" rather than to its "representativeness"; ² The figures in column 1 are based on mapped vegetation complexes within the System Six boundary (see Anon. 1993). The figures in column 2 are based on the total area of vegetation complexes depicted in maps published by the former Department of Conservation and the Environment (Heddle *et al.* 1980). The issue of conservation reserves in the Collie Coal Basin is being addressed by a detailed "Structure Plan". Complexes in the Drummond Botanical Sub-district (Swan Coastal Plain Bioregion) are excluded because they are outside the scope of this review.

1), concluding that there was no representation of those vegetation complexes in the northern jarrah forest that are centred in the adjacent regions and have been desirable acquisitions for agriculture since European settlement (Helena, Williams River). The Forrestfield vegetation complex, which straddles the western edge of the Jarrah Forest Bioregion, and Cardiff (on the Collie Coal measures) were also unrepresented.

Havel's analysis also showed that the agriculturally-desirable complexes centred in the northern jarrah forest had less than 5% representation (Wilga, Lowden, Michibin and Darling Scarp), as did the Muja vegetation complex of the Collie Coal Basin. Furthermore, Collie (the third complex of the Collie Coal Basin) was 5-10% reserved, as were the remaining complexes listed in Table 1, from:

- the lateritic uplands and shallow valleys in the western high rainfall zone — Dwellingup and Yarragul respectively.
- rocky valleys in the eastern low rainfall zone; Coolakin, and
- deep major river valleys; Murray (L/M) and Murray (M/H).

Havel (1989, pp 387-89) showed that the rest of the vegetation complexes had higher percentages reserved. These included the complexes;

- on lateritic uplands of the low to medium rainfall zone, and in the shallow valleys and depressions in the high to moderate rainfall zone (10 - 15%);
- on uplands and in the shallow valleys of the eastern low rainfall zone, and
- on infertile sands, steep rocky slopes of the monadnocks and swampy headwaters of the streams, as well as certain complexes of eastern dry lateritic uplands and of the deep valleys in the medium to high rainfall zone (20%+).

Generally, the coverage by conservation reserves within the forested landscape was found to be greater in the east than in the west of the region, and better on the extreme and less productive parts of the landscape than on the more productive ones. Historically, alienation for agriculture preceded both conservation and forestry, thereby limiting the opportunities for subsequent reservation.

Anon (1994) updated Havel's analysis, although somewhat different study area boundaries were used (Table 1). Since these assessments, the coverage of suitable environmental maps has been extended across the Blackwood Plateau and Manjimup areas in the south-west of the Jarrah Forest Bioregion (Tille & Lantzke 1990 and Churchward 1992, respectively), and through south coastal areas from Northcliffe to Manypeaks (Churchward *et al.* 1988) which includes the south-eastern corner of the Jarrah Forest Bioregion. In broad geographical terms, the currently recognised forest, woodland and shrubland communities that are least conserved by reserves are those:

- on the western margin of the Dale Sub-district (=Darling Scarp),
- agriculturally desirable surfaces throughout,
- the Collie Coalfields, and

- the north-western 30% of the Menzies Sub-district (=Blackwood Plateau) (Havel 1989 p 387; Keighery 1990).

Discussion

Gradients in community species composition

The problems of "land-class" approaches to reserve assessment mainly derive from assumptions of homogeneity and determinism, and have been reviewed by McKenzie *et al.* (1989). Intuitive regionalisations (land-classes such as land-systems, land-units and structurally based vegetation complexes) allow large areas to be surveyed quickly and are objective (Pressey & Nicholls 1991), but are insufficient from a biodiversity perspective because they usually reflect some mixture of vegetation patterns, topography, lithology and/or climate. This does not necessarily reflect the pattern of the entire biota (or even an "averaged" pattern), and does not quantify or map internal heterogeneity (McKenzie 1984; Margules *et al.* 1991; Pressey & Bedward 1991; McKenzie *et al.* 1992). In fact, land-classes are unlikely to be internally homogeneous and their boundaries may not be meaningful for many of the species in the region. The approach lacks spatial resolution because the relationships between the four layers (vegetation, topography, lithology and climate) are usually undefined in quantitative ways, and attributes such as species are not necessarily present at any point at any one time. This means that the generated data-base is intractable for more detailed analyses of ecological patterns. At fine scales, intuitive regionalisations also assume that compositional patterns are static, which they certainly aren't for mobile vertebrates.

Thus, land-class approaches provide only a first approximation of biological diversity patterns, and the reserve network should be subsequently refined using the ecological realism offered by quadrat strategies of data acquisition (McKenzie & Sattler 1994). Point data-sets derived from quadrat sampling strategies provide the spatial resolution that is needed to address the continuous gradients underlying ecological patterns, and allow us to compare sites quantitatively (Margules & Austin 1994). These data allow species with similar responses to environmental attributes to be clustered so that patterns in species composition across landscapes can be modelled for reserve design, and the predictions can be tested (Margules & Nicholls 1994; McKenzie *et al.* 1989 1991). Although quadrat sampling strategies are slow and expensive, significant cost-savings are offered by "gradsec" approaches to quadrat stratification (Gillison & Brewer 1985; Austin & Heyligers 1989) that systematically sample regions along major environmental gradients.

Quadrat data from surveys in different study areas (e.g. districts) can be combined into a geographically more extensive data-base without loss of spatial resolution, and quadrat-data also provide a basis for monitoring future changes (McKenzie *et al.* 1991a).

Jarrah forest context

The recent reviews of the conservation reserve system

in the northern jarrah forest have concluded that a thorough assessment of this reserve system's coverage in terms of the study area's biodiversity was not possible with available data (Havel 1989; Wardell-Johnson & Nicholls 1991). Havel (1989, p. 389) pointed out;

The already barely adequate representation of Yarragil (M/S) becomes even more critical when it is recognised that some of the component site-vegetation types, such as W and D, occur in topographical positions which render them susceptible to dieback infection, and contain a number of species which are highly vulnerable. This is also true of the Muja and Collie vegetation complexes.

According to the National Forest Policy Statement (NFPS 1992, p. 49) forest reserve systems should be assessed using three criteria;

1. comprehensiveness: include the array of community-types,
2. adequacy: ecologically viable and maintain integrity of populations, species and communities, and
3. representativeness: reasonably reflect the biotic diversity of each community.

While contemporary reserve selection algorithms can use land-class data to address "comprehensiveness" (Pressey & Nicholls 1989, 1991), data with more spatial and biological resolution are required to address "adequacy" and "representativeness" (Margules *et al.* 1991; Woinarski & Norton 1993; McKenzie & Sattler 1994).

Detailed knowledge of species biology and community dynamics and regional context are required to assess adequacy. Standardised, point-based data-sets that encompass a wide variety of organisms are required to assess representativeness. Wardell-Johnson & Nichols (1991) discuss this subject in a south-western forest context. While such data sets have been collected in parts of the forest (e.g. at Boddington, Worsley 1985), the problem is that they are too localised, and/or limited to a particular sort of organism (e.g. endangered plants, Kelly *et al.* 1990; birds, Wykes 1983; ants, Majer 1980).

Havel (1975) collected the most geographically extensive point-based data set, but his sampling concentrated on uplands and was confined to a selection of perennial plants. Granite outcrop, alluvial flat and heathland communities were under-represented, while annuals, perennials such as orchids, vertebrates, invertebrates, and the rarer components of the flora were all ignored (Havel 1989, p. 384).

Conclusion

We concur with previous reviews - the reserve system has already been assessed in terms of its comprehensiveness over most of the Jarrah Forest Bioregion. As yet there is no quantitative basis for assessing the reserve system's representativeness in terms of the jarrah forest's biodiversity at a level equivalent to that now possible in remote areas such as the Nullarbor (McKenzie *et al.* 1989), Western Australia's Eastern Goldfields (e.g. How *et al.* 1988; Burbidge *et al.* 1995) and Kimberley rainforests (McKenzie & Belbin 1991), and South Australia's Gawler Ranges (Robinson *et al.* 1985).

A quantitative biogeographical survey would provide

a model of the area's biological patterns from an ecosystem perspective. Such a survey would be quadrat-based and cover the major geological and geographical gradients in the area. At each quadrat, detailed sampling would need to cover different components of the biota that could be reasonably expected to be responding to different scalars. Typically such a survey would include vascular flora, small mammals, birds, reptiles and amphibians and selected invertebrate and cryptogram groups for which a good taxonomic basis exists.

Such data allow the development of regional models of gradients in the species composition of communities (quantified regional contexts) and allow decisions concerning land-use and management to be more explicit (McKenzie 1988). Such an approach would allow a more representative regional conservation network to be designed, one that could be expected to better represent the genetic resources of the widespread elements of the biota. It would not achieve adequate representation of the rare or restricted elements of the biota, for which the program of specific studies will need to continue in parallel.

Regional priorities have to be considered in proposals for major biogeographical surveys. There are 25 other biogeographical regions in Western Australia, and large-scale biogeographic surveys are expensive in terms of time, and in human and financial resources (Burbidge 1991). In the last 15 years it has not been practical to conduct more than one such survey at a time. Each survey requires up to 15 people during the fieldwork, and five people during the analysis and write-up phase for a period of 3 to 5 years. Recent analysis of the reservation status within the 26 bioregions recognised in Western Australia (Thackway & Creswell 1995) showed that 17 have a smaller proportion of their area reserved than the Jarrah Forest Bioregion, and 11 of these have a more biased reserve system (this means that entire sub-regions, or many of the extensive ecosystems that characterise a region, are missed). All of these regions can be considered much less resilient than the Jarrah Forest Bioregion.

From a biodiversity perspective at a state-wide scale, the Jarrah Forest Bioregion does not have a high priority for ecological survey. Nevertheless, the appraisals reviewed in this paper have identified gaps in the existing reserve system, even at the level of its comprehensiveness. These gaps relate to certain vegetation complexes on the Darling Scarp, the Blackwood Plateau, the Collie coalfields, and on agriculturally desirable soils. They should be addressed as a priority during the implementation of the National Forest Policy Statement (NFPS 1992).

Acknowledgements: We thank I Abbott, A Burbidge, A Hopkins, N Marchant and G Stoneman for their helpful comments on the draft. This review was updated from notes compiled in 1991 by N L McKenzie, S D Hopper and G Wardell-Johnson.

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A floristic survey of the Tingle Mosaic, south-western Australia: applications in land use planning and management

G Wardell-Johnson¹ & M Williams²

¹Science and Information Division, Department of Conservation and Land Management, PO Box 51 Wanneroo, WA 6065. present address, Department of Biology, University of Namibia, Private Bag 13301, Windhoek, Namibia. ²Science and Information Division, Department of Conservation and Land Management, Research Centre, Hayman Road, Como WA 6152

Abstract

A floristic survey of the Tingle Mosaic, an area of 3 700 km² which includes the wettest, least seasonal and southern-most part of Western Australia recorded a total of 857 vascular plant taxa in 441 quadrats (20 m x 20 m). These included 825 indigenous and 32 introduced taxa. Important families included the Papilionaceae (74 species), Proteaceae (73), Myrtaceae (64) and Orchidaceae (63).

Cluster analysis and ordination techniques defined five floristic communities supergroups, 12 community groups and 44 community types. The Open-forest, Tall open-forest and Shrubland/woodland Communities Supergroups included most of the quadrats (356 of 441), and also occupied the largest areas within the region. There was high alpha diversity for the Woodland and Open-forest communities supergroups, while there was low alpha and gamma diversity for the Tall open-forest Communities Supergroup. Considerable variation in vegetation structure, and high gamma diversity was found for the three non-forest communities supergroups. An expanded program of survey would be required to target the exceptional variety of sites in the Swamp and outcrop Communities Supergroup. The Tingle Mosaic had high levels of local endemism, many taxa (both wet and dry country taxa) which have range limits in the area, and several relictual high rainfall taxa whose distributions are centred in the area. A high proportion of the region lies within the conservation reserve network. Nevertheless the conservation significance and complexity of the fine-scale biotic pattern in the area urge increased attention in management and policy for the conservation of biodiversity. Methods to integrate site-based work, to define complexes of community types, and of the mapping of these floristic assemblages are presented. These applications would be invaluable in management for the conservation of biodiversity in the region.

Introduction

The south-west of Western Australia includes an extraordinary diversity of vascular plants in a generally subdued landscape (Hopper 1979; Hopper *et al.* 1992). This diversity has been especially noted for the inland transitional rainfall zone (TRZ *sensu* Hopper 1992) which is dominated by speciose genera of woody perennials in families such as the Myrtaceae, Proteaceae, Fabaceae and Epacridaceae (Hopper 1979; 1992) but not the high rainfall zone (HRZ) closer to the coast. Nevertheless wetland monocotyledonous taxa, including genera of Cyperaceae, Xyridaceae, Juncaginaceae, Restionaceae and Orchidaceae, are species-rich in the region. For example at least 1947 taxa are known from the Warren Botanical Subdistrict alone, despite limited survey (Hopper *et al.* 1992).

The HRZ is also notable for its high diversity of eucalypts compared with similar areas elsewhere in the Darling Botanical District (Christensen 1980; Smith *et al.* 1991, Wardell-Johnson & Smith 1991; Wardell-Johnson & Coates 1996, Wardell-Johnson *et al.* in press). At least

four species of large forest eucalypts, *Eucalyptus brevistylis* (Rates tingle), *E. jacksonii* (red tingle), *E. guilfoylei* (yellow tingle), and *E. ficifolia* (red-flowering gum) are locally endemic to the south-west between Walpole and Denmark. Each occurs in several allopatric populations in an area of high landscape and vegetation structural diversity. Because it was the tingles that first drew attention to the conservation significance of this landscape mosaic (Ferne & Fernie 1989), the survey area is described as the Tingle Mosaic.

The Tingle Mosaic is also notable for its scenic diversity and has been the subject of intense public interest (Smith *et al.* 1991; Wardell-Johnson & Smith 1991; Wardell-Johnson & Horwitz 1996). It occurs in close proximity to the towns of Walpole, Denmark and Albany (Smith *et al.* 1991) but includes areas that are generally remote and have not been explored botanically. The vascular flora has been chosen for study because of its richness (Hopper *et al.* 1992) and because of its propensity to describe landscape pattern (Havel 1981; Wardell-Johnson *et al.* 1989). The identification and classification of plant community types is a useful first step in land-use planning (Havel 1981; Wardell-Johnson *et al.* 1989). This allows the identification of rare or vulnerable communities at a regional level and allows a management context to be provided. Historically, vegetation classification in Australia has been based on a structural or physiognomic basis (Diels 1906; Speck 1952; Webb *et*

al. 1976; Beard 1981). More recent work has utilised floristic attributes (e.g. Havel 1975a,b; Webb *et al.* 1984; Cresswell & Bridgewater 1985; Foran *et al.* 1986). However, the final choice of attributes used to classify vegetation remains a function of the aims of the research project at hand (Anderson 1981).

Here, we describe the variation in the floristic composition of the area within the range limits of four locally endemic forest eucalypts (Tingle Mosaic) and identify sites with similar species composition (community types; terminology after Whittaker 1973).

Methods

Study area

The study area in south-western Australia lies between latitudes $34^{\circ} 45'$ and $35^{\circ} 10'$ and longitudes $116^{\circ} 30'$ and $117^{\circ} 45'$. This area of approximately 3 700 km² (Table 1, Fig 1) within the Warren and Menzies Botanical Subdistricts of Beard (1980) includes the wettest and least seasonal part of Western Australia, although isohyets decline rapidly eastwards and from the coast.

Peter Tille (Agriculture WA, pers. comm., 1995) defined 98 land systems within 16 zones for The Darling Botanical District of Beard (1980), based on geology and recurring landform patterns. This area includes almost all of the jarrah and karri forests and woodlands of

south-western Australia. The Tingle Mosaic lies within three zones (the Warren-Denmark southland, the Stirling coastal, and the Stirling Sandplain) and nine Land systems. The area includes two geomorphic provinces within the South-west Land Division (the Avon and the Stirling).

Climate

The region has a mediterranean climate (Gentili 1971) with dry, generally temperate summers and cool, wet winters. The high rainfall parts of the Tingle Mosaic receive more reliable summer rain than elsewhere in the south-west. There is a considerable range in temperature and rainfall with gradients from both south-to-north and west-to-east. Thus in the south-western parts, annual rainfall exceeds 1 400 mm (Fig 1), whereas in the north-east it is about 750 mm.

Geology, physiography and soils

The Tingle Mosaic includes the southern fringe of the Great Plateau of Western Australia (Jutson 1914). It is composed of Precambrian granite rocks, partially overlain by various consolidated and unconsolidated sediments. This land surface has been subjected to a long and complex history of weathering and denudation which is expressed as variations in topography, soils and hydrology.

These factors, together with the nature of the rock

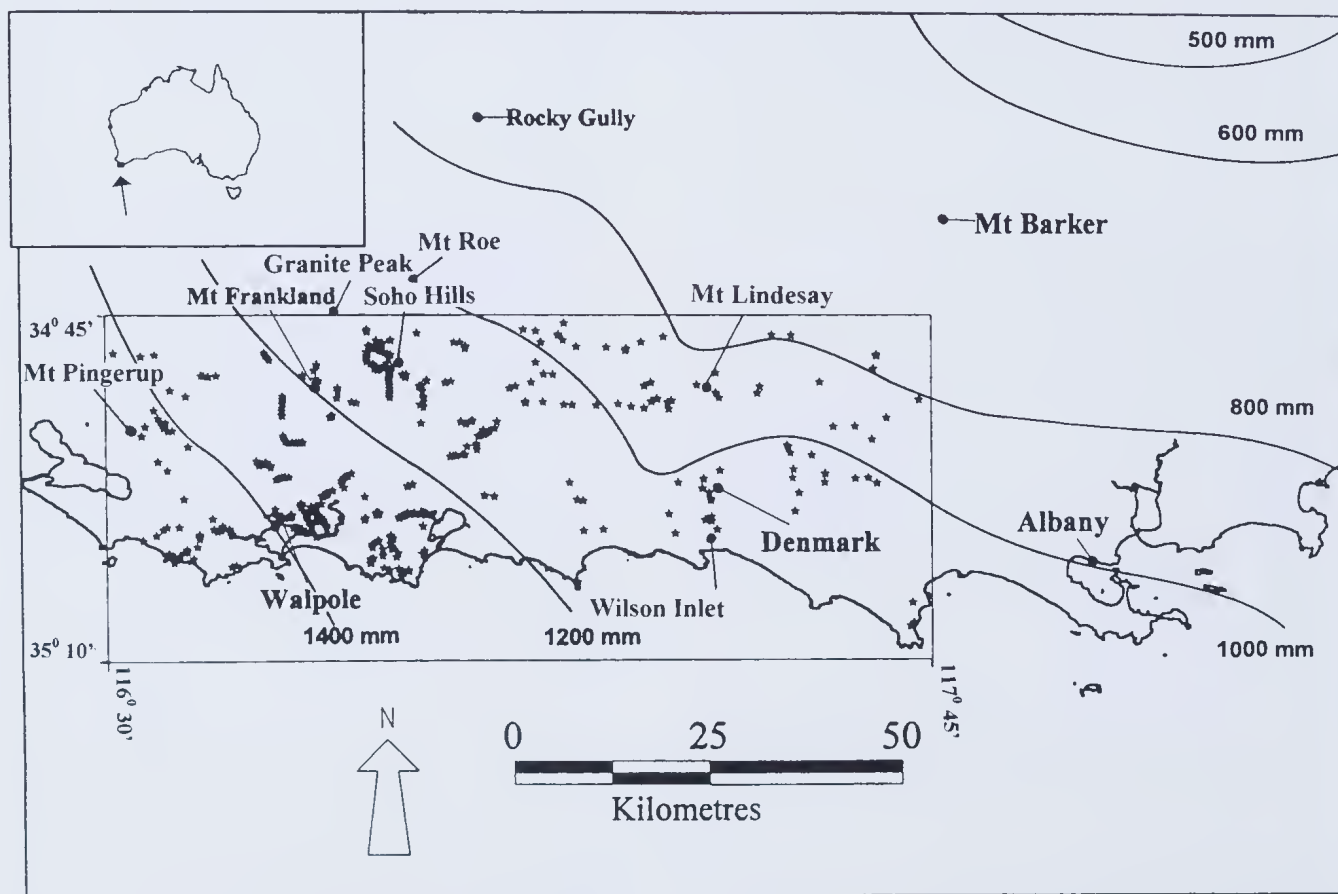


Figure 1. Study area showing the distribution of permanently located floristic quadrats, isohyets and major towns in south-western Australia.

Table 1

Tenure context of survey area. Reserves are National Parks, Nature Reserves and Conservation Parks. State Forest includes Executive Director lands, Timber Reserves and Other Reserves.

Location	Reserves km ² (%)	State Forest km ² (%)	Other km ² (%)	Private Land km ² (%)	Total Area km ²
Darling Botanical District	8 070 (11.3)	16 100 (22.6)	1 100 (1.5)	46 060 (64.6)	71 300
Warren Botanical District	2 870 (27.8)	3 290 (32)	430 (0.9)	3 709 (36)	10 300
Tingle Mosaic	909 (24.6)	686 (18.5)	387 (10.4)	1 717 (46.5)	3 700

types, formed the basis for the recognition of the landform/soils units defined and described by Churchward *et al.* (1988). These authors provided a detailed set of five 1:100 000 scale landform and soils maps covering an area between Windy Harbour eastward to Cheyne (Hassell) Beach, 80 km east of Albany, and extending inland to latitude 34° 31' S (as far north as Rocky Gully). Thirty-five units were mapped, based firstly on general geological features (*i.e.* units developed on granite or unconsolidated sediments, on siltstones and sandstones, on coastal aeolian and fluvial sediments and on drainage lines), and then on landform (plateau elements, hills and ridges, swampy terrain, dune systems, and major and minor valleys). They also provided further subdivision into individual units based on soils, local relief, slope and drainage patterns. The maps of Churchward *et al.* (1988) provided a sound context for stratification in this survey (and also for broad-scale ecosystem management in the area).

Most of the Tingle Mosaic has soils which are developed on components of laterite profiles either exposed by erosion or as colluvial waste released by this process. Many of these soils have ferruginous gravels in the surface horizons. In the unconsolidated sandy sediments, soil morphology is influenced mainly by drainage status, while in the coastal sand dunes, soil variation often relates to the age of parent material.

The headwaters of the Frankland River, a large river which rises well to the north of the Tingle Mosaic, are in broad valleys with salt lakes. Hence, there is a natural contribution of salts to the surface water. This is at a maximum following heavy winter rains. The headwaters of the Deep, Denmark, Kent and Hay Rivers also rise to the north of the Tingle Mosaic, and occur in areas with high soluble salts in the subsoil. Surface incidence of salinity is most evident in the north-east part of the Tingle Mosaic, and is expressed both as seepage on slopes and as saline valley floors. Salinity is not apparent on the plateau developed on marine sediments even though rainfall is low and the substrata known to be saline (Teakle 1953).

The general level of the Great Plateau gradually falls toward sea level in the area and forms part of the Ravensthorpe Ramp (Cope 1975). In the east, the landscape consists of a plateau developed on Pallinup Siltstone. The plateau surface represented by gently undulating plain slopes from about 180 m above sea level to about 40 m near the coast. In the remainder of the area, much of the terrain is developed on granitic rocks although there is a variable incidence of unconsolidated

deposits as well as westward extensions of the Eocene sediments. This is at an elevation of from 260 to 180 m above sea level and is part of the Great Plateau underlain by deeply weathered granite. Some broad sandy, often swampy tracts are included.

To the west, extensive tracts such as the Pingerup Plains grade in elevation from 70 m inland, to less than 20 m where they abutt the narrow zone of coastal dunes. Granite is sometimes exposed as domes and pinnacles emergent above the sandy tracts (*e.g.* Mt Pingerup). The terrain is dominated by a pattern of ridges of granitic rocks alternating with broad swampy corridors, having a west-north-west orientation. The crests of many of the ridges are in excess of 100 m above the corridors.

On the coastal fringe, both Precambrian and Tertiary rocks are overlain by Tamala Limestone of Pleistocene age (Logan 1968) and/or unconsolidated Holocene aeolian sands. The broad ridges of Tamala Limestone rise to about 100 m and often act as barriers behind which estuaries, such as Wilson Inlet, have developed. A system of Holocene parabolic dunes extend from the coast in a general east-north-east direction, overlying the broad ridges of limestone and of granite as well as alluvial and estuarine deposits. Much of the coastline is characterised by a succession of arcuate bays with granitic headlands linked by the barriers of Tamala Limestone in which steep cliffs have usually been cut. Most of these bays face south-west. The coastal plain in the immediate hinterland of the dunes is mantled by unconsolidated alluvium and/or aeolian sands.

Vegetation

Each of the 35 landform units defined by Churchward *et al.* (1988) were described in terms of their physiography, geology, soil morphology and associated native vegetation. The latter was described structurally, and dominants were listed for each major stratum. This provided a means of determining quadrat locations to ensure a regional coverage of a complex area. The natural vegetation of the area has been mapped (scale 1:250 000) by Smith (1972) and Beard (1972-80).

Hopper *et al.* (1992) provided a regional perspective for the flora of the Warren Botanical Subdistrict. They listed 1947 taxa including 1628 native and 319 naturalised introduced taxa for the area (roughly equivalent in size to the Perth Region; 8323 km² extending over 300 km from Yallingup on the Leeuwin-Naturaliste Ridge to Albany on the south coast).

Many site-based floristic studies have been carried out, in or nearby to the Tingle Mosaic. For example,

Strelein (1988) presented an ordination using over 400 sample sites and 100 indicator species in the southern jarrah forest. He defined seventeen site types from this work using the methods of Havel (1968, 1975a,b) and discussed the regeneration, dieback susceptibility and productivity of each. Inions *et al.* (1990) derived a floristic classification of regenerating karri forest in the Nornalup System of the Warren Subdistrict. They used 204 permanent inventory plots (Campbell *et al.* 1985) and 105 species were sampled. Thirteen community types were defined by cluster analysis, ordination and discriminant analysis of the 312 m² quadrats. Wardell-Johnson *et al.* (1989) developed a floristic classification of the Walpole-Nornalup National Park based on 219 quadrats and 233 species. Twelve community types were derived with clustering and ordination techniques. Several smaller site-based studies have also been carried out in the area (e.g. Hopkins & Griffin 1984). These have been reviewed by Hopper *et al.* (1992). Other opportunistic flora surveys have been carried out in the area over many years and a preliminary list of flora for the Warren Botanical Subdistrict is now available. Thus, over 2200 indigenous vascular plant taxa, many yet to be named, are known from this subdistrict alone (Hopper *et al.* 1992; N Gibson, CALM *pers. comm.* 1995).

Sampling sites

This study was based on intensive sampling of the different vegetation types in representative areas. Areas were chosen on the basis of the landform/soils classification of Churchward *et al.* (1988), although more intensive survey in the Walpole-Nornalup National Park was completed prior to the availability of this work (but see Wardell-Johnson *et al.* 1989). Data from 144 sites of quadrat size 10 m radius (312 m²) have been included from this work (see also Wardell-Johnson *et al.* 1989). Hence the survey effort is considerably greater for the WNNP than for the remainder of the Tingle Mosaic. The park does however include a major proportion of the populations of all three tingles as well as *E. ficifolia* (Smith *et al.* 1991, Wardell-Johnson & Smith 1991). Hence the concentration of quadrats in this area reflects the concentration of the rare eucalypts in the area.

The locations of sampling sites were selected to give as wide a range as possible of vegetation types from throughout the study area. All quadrats were located in undisturbed indigenous vegetation, with few weeds occurring in the area and no recent history of high intensity fire. Sampling preference was given to areas which were in existing conservation reserves rather than private property or road reserves.

Detailed studies have recognised that an appropriate sample area is about 400 m² in forested areas (Burbidge & Boscacci 1987; D Keith, Forests Commission of NSW, *pers. comm.* 1994). This allows a representative floristic list for the site, and minimises the influences of individual large trees or logs within a quadrat. Quadrats larger than this risk encountering ecotones in the diverse vegetation of the HRZ of south-western Australia. All quadrats in this study were 20 m x 20 m, except those from the Walpole-Nornalup National Park survey mentioned above. All quadrats were established and permanently marked in the field by metal star pickets at centre points, and droppers at corners. The sites were checked

at least twice, including at least once in spring. Species nomenclature follows Green (1985).

Analytical techniques

All sites (441) and all taxa (857) were analysed for plants presence/absence, which provides most of the information by ordination and classification of site-based data (Anderberg 1973). A matrix of pairwise associations between sites was calculated using the Czekanowski (1913) metric. UPGMA (Sneath & Sokal 1973) was used to derive clusters from the dataset; although this is sometimes prone to minor misclassification, it has the advantage of taking more than one species into account at any fusion. The clustering-intensity coefficient beta (β) was -0.10; under such conditions the clustering strategy is space-dilating and resists the formation of a single large group by forcing the formation of even-sized groups (Booth 1978).

The use of clustering techniques assumes that a population is discontinuous; the validity of this assumption depends on the species' response to environmental gradients and the nature of the gradients themselves (Austin & Cunningham 1981). In reality, vegetation is likely to vary from apparently continuous to apparently discontinuous with the nature of boundaries varying in width and level of diffusion throughout, and by how they are defined. The location of sample sites can also have an influence over the degree to which the vegetation of a region is considered continuous or discontinuous.

The acceptability of imposed groups was examined by ordinating the sites using semi-strong-hybrid multidimensional scaling (PATN; Belbin 1993), and examining the position of group members in component space. As analysis should not be performed across major data discontinuities (Green 1980), further cluster analysis was performed on each of the five major discontinuity's determined through initial analysis.

Results

Sites and species

A total of 857 vascular plant taxa were recorded in the 441 quadrats of the Tingle Mosaic. Important plant families included the Papilionaceae (74 species), Proteaceae (73), Myrtaceae (64) and Orchidaceae (63). Relative to the number of taxa represented in the Warren Botanical Subdistrict, the Orchidaceae (63), Cyperaceae (34), Restionaceae (34), Poaceae (24) and Asteraceae (19) were relatively poorly represented in quadrats (see Hopper *et al.* 1992). The largest representation of genera included *Acacia* (23 species), *Stylidium* (36), *Leucopogon* (20) and *Eucalyptus* (22). *Caladenia* (12) and *Drosera* (12) were relatively poorly represented in quadrats in comparison with the Warren flora as a whole. A list of the taxa and their constancy (proportion of quadrats in which the species is present) in community groups is presented in Appendix 1. Several name changes occurred during the course of the study, and several taxa were found to have been misidentified once multivariate analysis was complete. These were few, thus providing little likelihood of influencing the overall classification. They are also shown in Appendix 1.

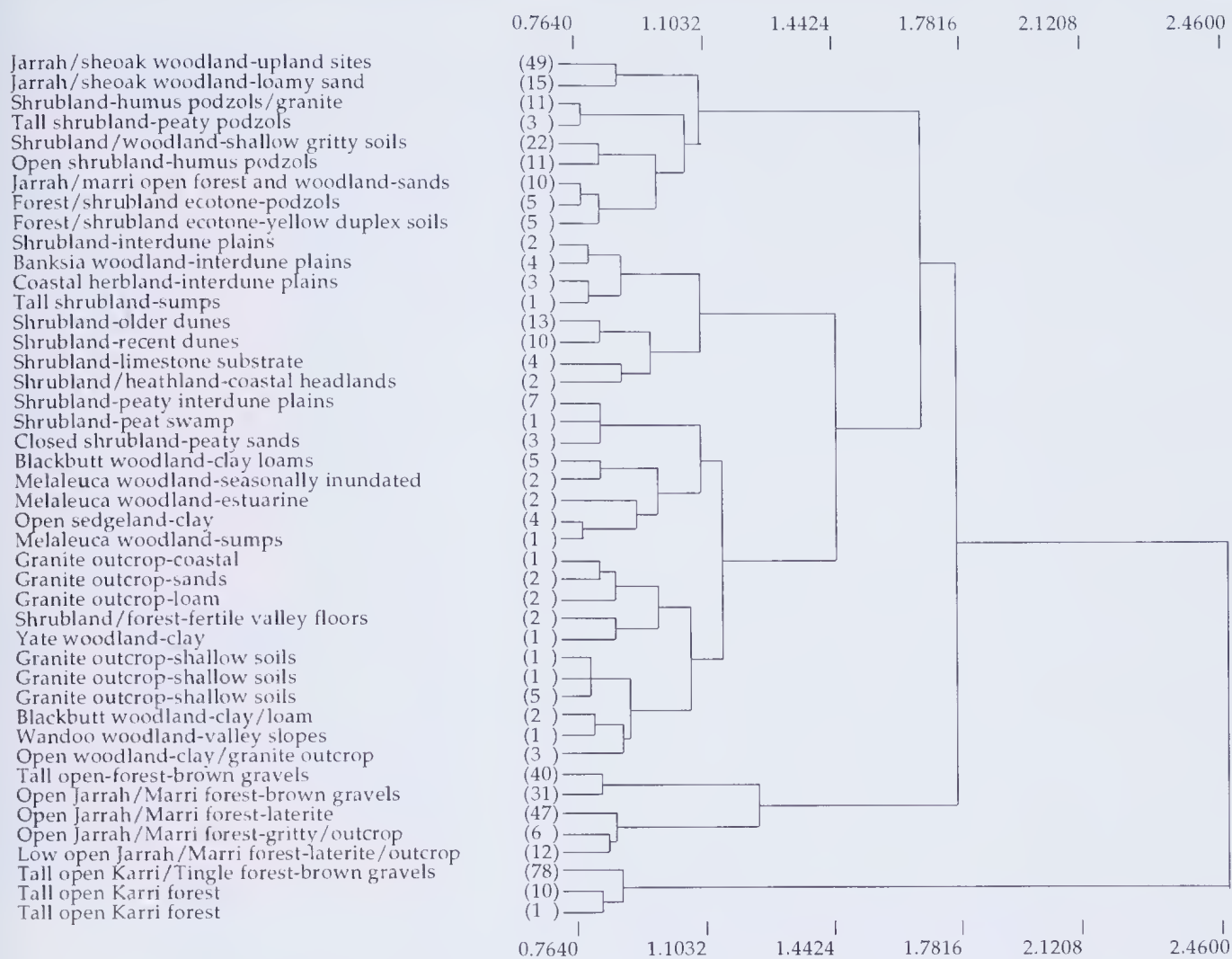


Figure 2. Dendrogram classification of 441 sites, based on 857 vascular plant taxa showing communities supergroups (A-E) and community types. The predominant vegetation and soil features of the 44 community types are shown with numbers of quadrats in brackets. Reprinted from Wardell-Johnson & Horwitz (1996) *Forest Ecology and Management*, 85(1-3), Conserving biodiversity and the recognition of heterogeneity in ancient landscapes: a case study from south-western Australia, 219-238, 1996 with kind permission of Elsevier Science - NL, Sara Burgerhartstraat 25, 1055 KV Amsterdam, The Netherlands.

Cluster analysis and ordination defined five floristic communities supergroups, 12 community groups and 44 community types (Figs 2-3; Table 2). As the five communities supergroups represent a clear discontinuity in both cluster analysis and ordination, it is likely that this will mask differences amongst community types (Green 1980). Thus the five communities supergroups were each analysed separately for higher resolution within the supergroups and to define community sub-types.

A clear separation of sites at the 12 group level defined groups of similar sites according to broad topography, drainage and soils characteristics. These 12 groups are referred to as community groups and the constancy of taxa within these groups are presented as a summary of the floristics of the area (Appendix 1). All but the tall open-forest communities supergroup comprise more than one community group.

Shrubland/woodland Communities Supergroup. (A: 131 quadrats and 464 taxa) included four community groups (forest/sandplain ecotone sites, woodland

communities in shallow soils, shrubland on sandplains, woodland on sandy crests and valley divides), nine types and ten sub-types (Fig 4, Table 3). These were generally sites in broad sandy terrain.

Dune Vegetation Communities Supergroup. (B: 39 quadrats and 268 taxa) included two community groups (Merrup Dunes, Interdune plain and swamp), eight types and ten sub-types in aeolian dunes (Fig 5, Table 4).

Swamp and outcrop Communities Supergroup. (C: 46 quadrats and 524 taxa) included three community groups (wandoo woodland and outcrop, saline swamps, and peat swamps) and 19 types (Fig 6, Table 5). These sites were in swampy terrain or areas of impeded drainage or outcrop. The limited sampling and heterogeneity of these community types prevented assessment below the 19 group level.

Open-forest Communities Supergroup. (D: 136 quadrats and 428 taxa) included two community groups (jarrah/marri/tingle open-forest, jarrah/marri open-forest), five types and 14 sub-types (Fig 7, Table 6).

Table 2
Summary statistics of communities supergroups and community groups of the Tingle Mosaic.

Community supergroup	Community types	Sub-community types	taxa	quadrats	Community group (community types)
A: Shrubland/woodland communities	9	10	464	131	A1: Forest/sandplain ecotone sites (3) A2: Woodland communities in shallow soils (2) A3: Shrubland on sandplains(2) A4: Woodland on sandy crests and valley divides (2) Walpole, Kentdale, King, Broke, King (swamps, plateau, valley divides)
B: Dune vegetation	8	10	268	39	B1: Merrup Dunes (4) B2: Interdune plain and swamp (4) Nullakai (dunes)
C: Swamp and outcrop	19	19	524	46	C1: Wandoo woodland and outcrop (11) C2: Saline swamps (5) C3: Peat swamps (3). All (swampy terrain, plateau and hills).
D: Open-forest	5	14	428	136	D1: Jarrah/marri/tingle tall open forest (2) D2: Jarrah/marri open forest (3) Walpole, Roe, Kentdale, King, Pardalup, King, Redmond (hills, ridges, plateau)
E: Tall open-forest	3	12	132	89	E1: Karri/tingle tall-open forest (3) Walpole (hills and ridges)

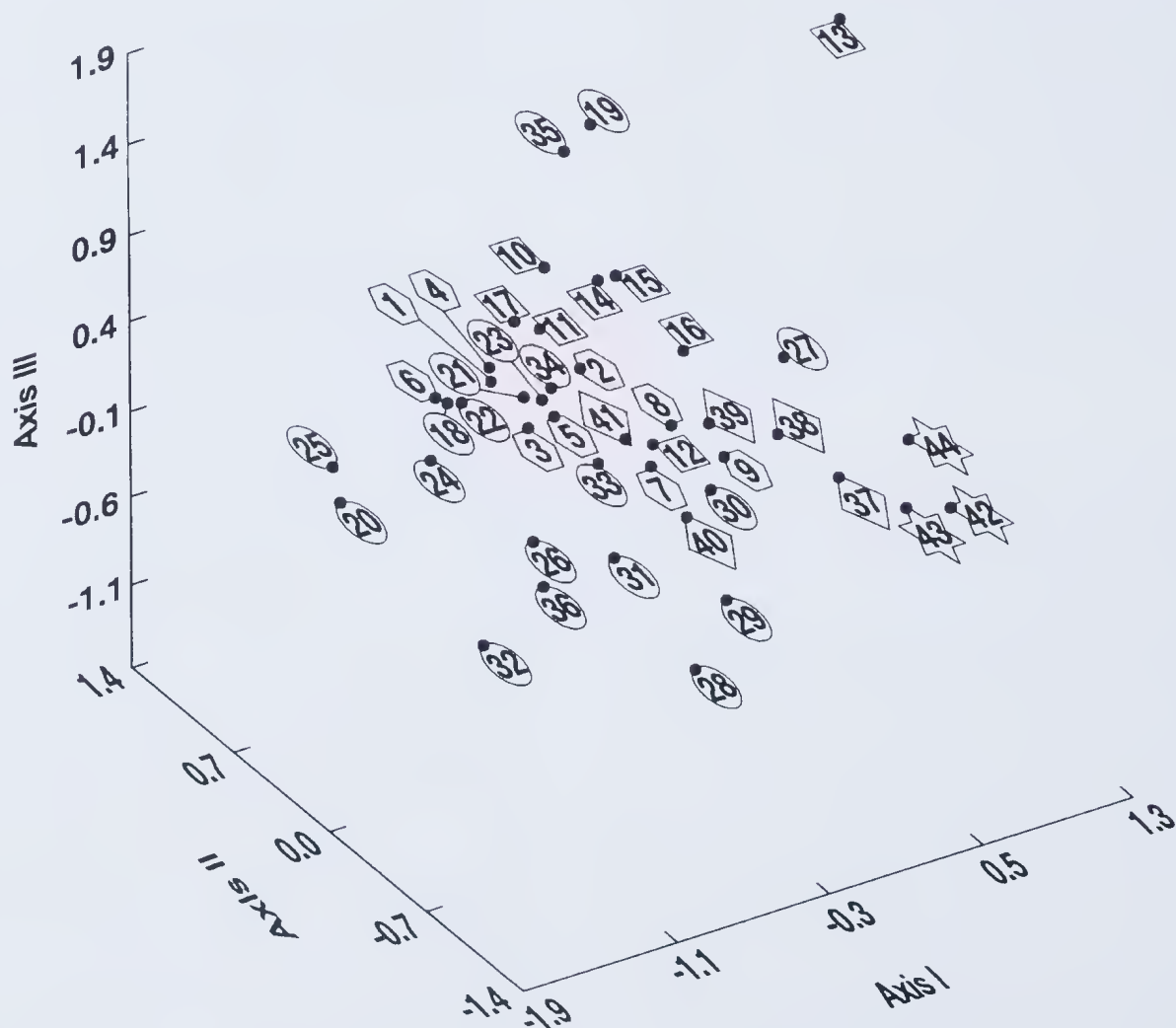


Figure 3. Centroids of the 44 community types clustered in three dimensions using semi-strong-hybrid multidimensional scaling.

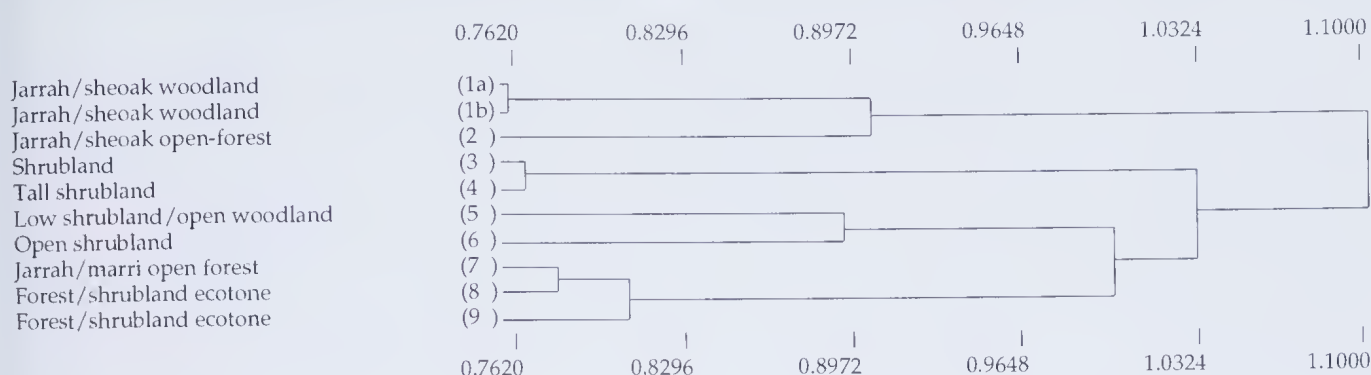


Figure 4. Dendrogram classification of the 131 sites (based on 424 vascular plant taxa) of the Shrubland/woodland Communities Supergroup (A); community type and sub-type are shown in brackets.

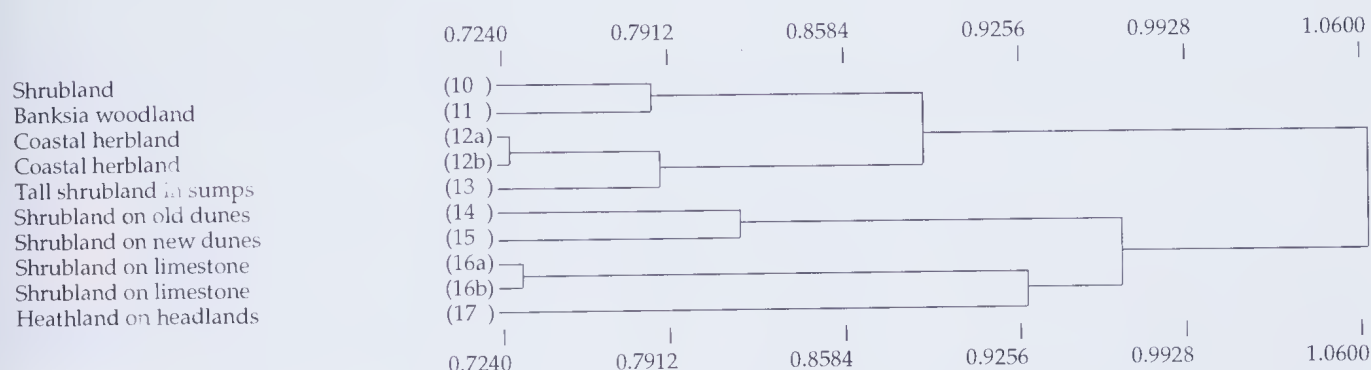


Figure 5. Dendrogram classification of the 39 sites (based on 241 vascular plant taxa) of the Dune vegetation Communities Supergroup (B); community type and sub-type are shown in brackets.

Table 3

Description of community types in Shrubland/woodland Communities Supergroup (Communities Supergroup A).

Community-type ^a	Description	Number of quadrats ^a	Species richness ^a	Landform/soils ^b
1(a,b)	Jarrah/sheoak	49 (39, 10)	43.0 (42.9, 43.6)	Freely drained sands in uplands and valley divides (CA, Bwp, Ds, Dc, Q).
2	Jarrah/sheoak open forest and woodland	15	36.3	Fertile sands with some loam (WA, CA, HA).
3	Shrubland to tall shrubland	11	23.4	Humus podzols in gently sloping sandy terrain (HA, A).
4	Tall shrubland	3	29.3	Peaty podzols in lower slopes of sandy terrain (HA, A).
5	Low shrubland to open woodland	22	47.2	Shallow gritty duplex soils/podzols (Lp, Kp, Mtp, Cop, BU).
6	Open shrubland	11	41.9	Humus podzols (F, CA).
7	Jarrah/marri open forest and woodland	10	40.7	Sands (HA, A).
8	Forest-shrubland ecotone	5	40.8	Leached sands and podzols (Gs, Ks).
9	Forest-shrubland ecotone	5	21.0	Sandy yellow duplex soils (A, HA)

^a values for sub-communities in parentheses; ^b units of Churchward *et al.* (1988).

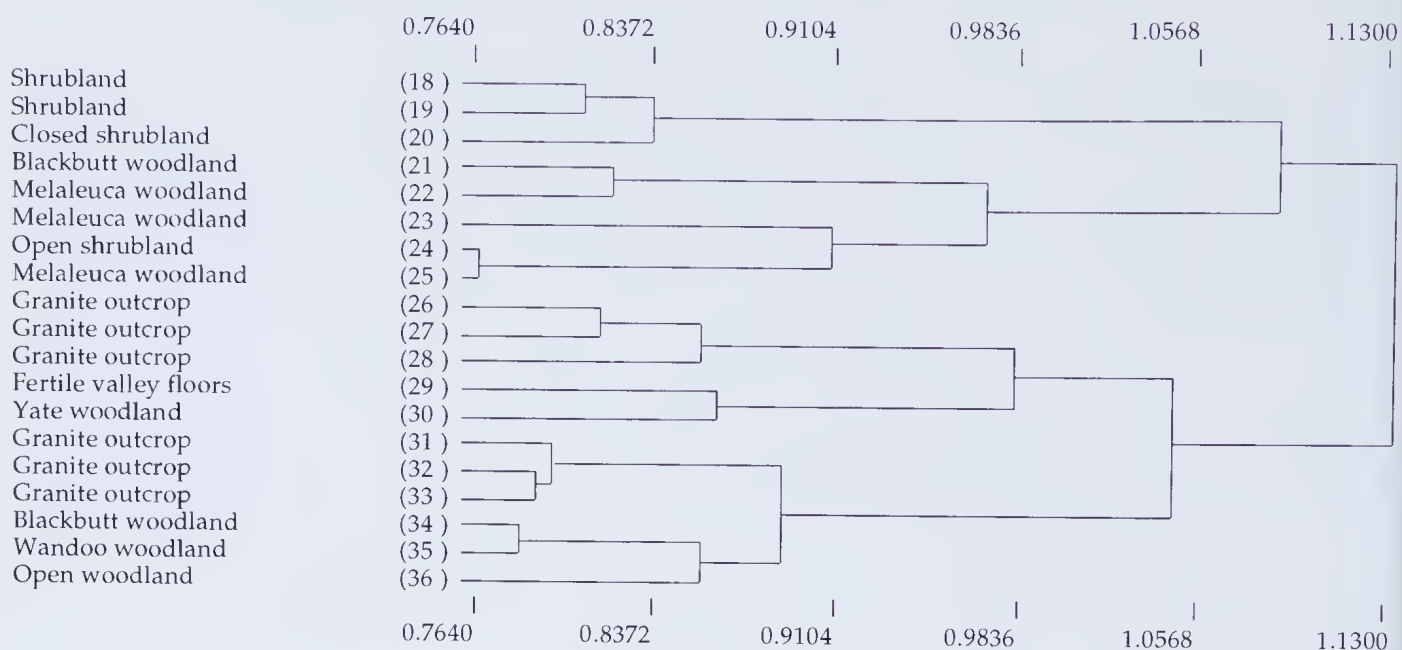


Figure 6. Dendrogram classification of the 46 sites (based on 524 vascular plant taxa) of the Swamp and outcrop Communities Supergroup (C); community type and sub-type are shown in brackets.

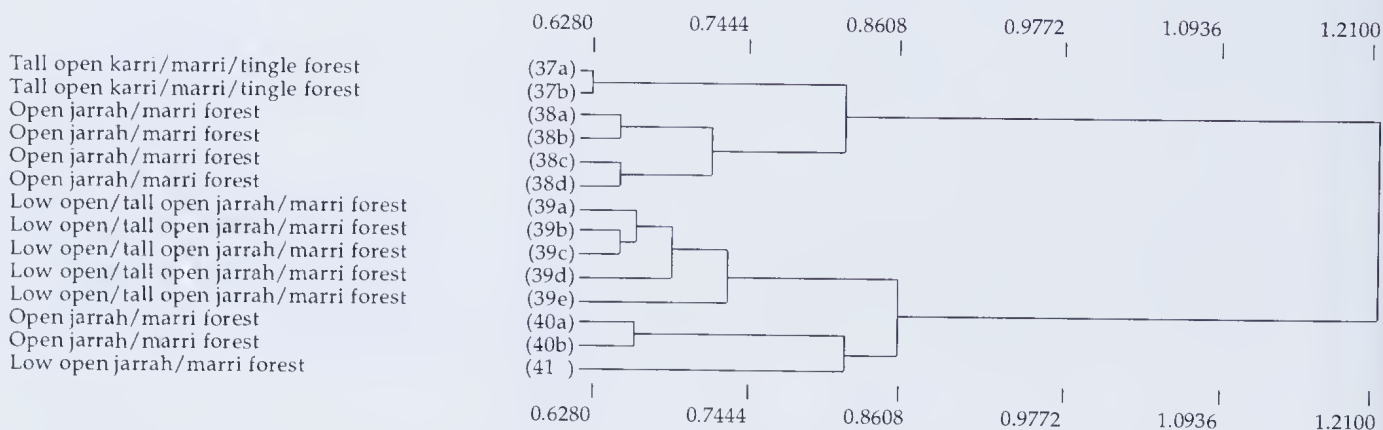


Figure 7. Dendrogram classification of the 136 sites (based on 428 vascular plant taxa) of the Open-forest Communities Supergroup (D); community type and sub-type are shown in brackets.

These were in hilly terrain, but with poor soils or moisture holding capacity

Tall open-forest Communities Supergroup. Separate community groups were not recognised in this community supergroup (E: 89 quadrats and 136 taxa). However, three types and 12 sub-types were defined in this supergroup (Fig 8, Table 7) which included sites occurring in loamy soils in freely drained upland areas with good moisture retention capabilities. Considerable variation in vegetation structure was noted in the three non-forest supergroups.

Community types and species richness

The Tingle Mosaic was rich in species, although quadrats in tall-open forest were species-poor (Table 7).

Species richness between quadrats was not normally distributed (Fig 9). This distribution reflected the uneven sampling effort within the study area. There was a large number of quadrats in tall open-forest with low species richness, and in open-forest and woodland with high species richness. Community types are species-rich in all but relatively fertile freely-drained upland sites, and extreme areas such as outcrop or saline seepage. Species richness is very high in open-forest and woodland environments on shallow or sandy soils.

The high richness of the Tingle Mosaic manifested itself through a very high proportion of singletons within quadrats of the survey area, particularly in the Open-forest and Swamp and outcrop Communities Supergroups. Notably, over 25 % of species occurred in only a single quadrat (singletons - Table 8). A high pro-

Table 4

Description of community types in the Dune vegetation Communities Supergroup (Communities Supergroup B)

Community-type ^a	Description	Number of quadrats ^a	Species richness ^a	Landform/soils ^b
10	Shrubland.	2	34.0	Interdune plains in older D'Entrecasteaux dunes Seasonally inundated, interdune plains in D'Entrecasteaux dunes.
11	Banksia woodland.	4	39.7	
12 (a,b)	Seasonally inundated coastal herbland.	3(1, 2)	27.3 (27.0, 28.0)	
13	Tall shrubland in sumps	1	20.0	Sumps in BWp.
14	Shrubland on older dunes.	13	40.1	Older D'Entrecasteaux dunes.
15	Shrubland on recent dunes	10	36.0	
16 (a,b)	Closed shrubland on limestone substrate	4 (1, 3)	26.5 (28.0, 26.0)	Recent D'Entrecasteaux dunes. Limestone substrate in D'Entrecasteaux dunes.
17	Open shrubland to low open heathland on coastal headlands	2	29.5	Coastal granite headlands in D'Entrecasteaux dunes.

^a values for sub-communities in parentheses; ^b units of Churchward *et al.* (1988).

Table 5

Description of community types in the Swamp and outcrop Communities Supergroup (Communities Supergroup C).

Community type	Description	Number of quadrats	Species richness	Landform/soils ^a
18	Shrubland.	7	39.1	Broad peaty interdune plains.
19	Shrubland.	1	28.0	Permanently moist freely drained peaty swamps.
20	Closed shrubland.	3	23.0	Broad seasonally inundated peaty sands
21	Blackbutt woodland.	5	40.2	Seasonally inundated clay loams.
22	Melaleuca woodland	2	35.5	Seasonally inundated.
23	Melaleuca woodland	2	24.0	Seasonally inundated estuarine habitats.
24	Open sedgeland.	4	24.7	Seasonally inundated clay soils.
25	Melaleuca woodland	1	20.0	Seasonally inundated sumps.
26	Granite outcrop.	1	29.0	Coastal granite outcrop.
27	Granite outcrop.	2	29.5	Sand amongst granite outcrop.
28	Granite outcrop.	2	17.0	Loam amongst granite outcrop.
29	Tall Shrubland to Tall open-forest	2	17.0	Fertile minor valley floors.
30	Yate woodland.	1	55.0	Clay valley floors.
31	Granite outcrop.	1	66.0	Shallow soils on granite outcrop
32	Granite outcrop.	1	39.0	Shallow soils on granite outcrop
33	Granite outcrop.	5	60.2	Shallow soils on granite outcrop
34	Seasonally inundated blackbutt woodland.	2	55.0	Clay-loams on seasonally inundated valley floors
35	Wandoo woodland	1	26.0	Low valley slopes
36	Open woodland.	3	43.0	Clay in granitic outcrop

^a units of Churchward *et al.* (1988).

Table 6

Description of community types in the Tall open-forest Communities Supergroup (Communities Supergroup D).

Community-type	Description	Number of quadrats ^a	Species richness ^a	Landform/soils ^b
37(a, b)	Tall-open karri/marri/yellow tingle forest	40 (12, 31)	34.0 (33.4, 38.7)	Brown/yellow gravelly freely drained upland (Ky, My, COy, V1)
38(a, b, c, d, e)	open jarrah/marri forest	31(3, 8, 6, 14)	42.8(55.7, 41.1, 42.5, 40.0)	Brown-gravelly freely drained upland (Kb, Mb, COb, V1)
39(a, b, c d, e)	Low-open to tall-open jarrah/marri forest	47(9, 17, 6, 9, 5)	53.5(65.2, 54.8, 50.3, 41.2, 45.8)	Gravelly upland sites - including block laterite (Ky, Kp, My, COy).
40(a, b)	Open jarrah/marri forest	6(5, 1)	47.5(46.0, 54.0)	Shallow gritty soils amongst rock outcrop (Ly, Ls, Lg, Ks).
41	Low-open jarrah/marri forest associated with granite outcrop.	12	55.4	Shallow gritty soils amongst rock outcrop with laterite (COp, COy Mtp, Mty, Ly, Lp).

^a values for sub-communities in parentheses; ^b units of Churchward *et al.* (1988).

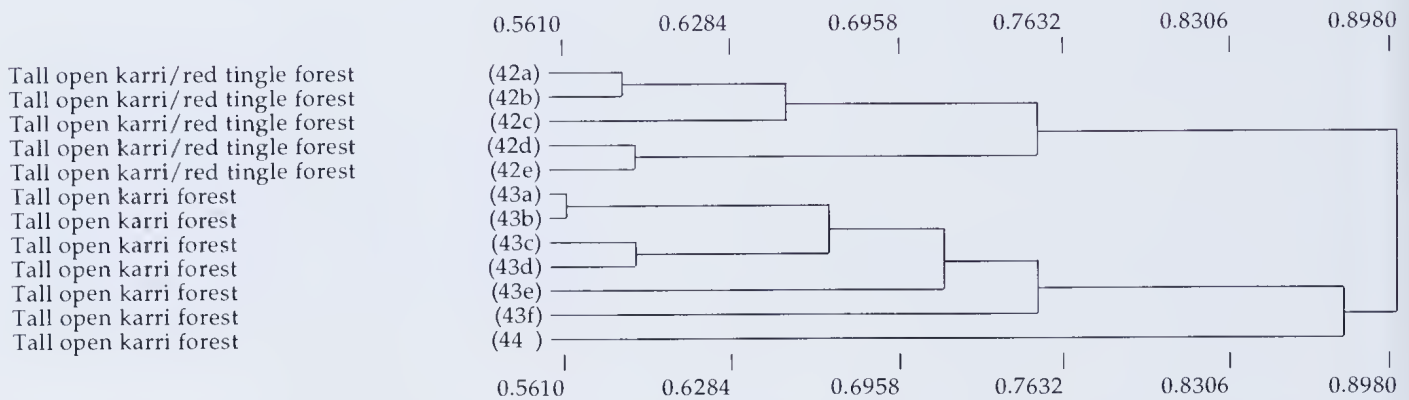


Figure 8. Dendrogram classification of the 89 sites (based on 132 vascular plant taxa) of the Tall open-forest Communities Supergroup (E); community type and sub-type are shown in brackets.

Table 7

Description of community types in the Tall open-forest Communities Supergroup (Communities Supergroup E).

Community-type ^a	Description	Number of quadrats ^a	Species richness ^a	Landform/soils ^b
42(a, b, c)	Tall-open karri/red tingle forest	78(12, 20, 10, 29, 7)	19.3(18.1, 21.8, 24.5, 17.0, 16.0)	Brown-gravelly freely drained upland (Kb, Mb, COb, V1)
43(a, b, c, d, e, f)	Tall-open karri forest	10(1, 1, 5, 1, 3, 1)	19.1(16.0, 25.9, 17.2, 15.0, 33.0 16.0)	Brown-gravelly freely drained upland (Kb)
44	Tall-open karri forest	1	12.0	Brown=gravelly freely drained upland (Kb)

^a values for sub-communities in parentheses; ^b units of Churchward *et al.* (1988).

Table 8

Comparisons between three floristic surveys of the high rainfall zone (HRZ) of south-western Australia.

Survey	Authors	Area km ²	Species (analysed)	Singletons (%)	Quadrats	Community types
Tingle Mosaic	Wardell-Johnson	3 700	(857)	214 (25)	441	44 (75 subtypes)
Swan Coastal Plain	Gibson <i>et al.</i> (1994)	4 000	1485 (1097)	272 (25)	509	30 (43 subtypes)
South Coast	Gibson (pers. comm.)	2 000	910 (877)	214 (24)	301	40

portion of singletons has also been noted in other floristic studies carried out in the HRZ (Table 8).

Endemism in the Tingle Mosaic

A total of 20 taxa, endemic to the Tingle Mosaic were encountered in quadrats located in this study area (Table 9). At least another 13 taxa are known to be endemic to the study area, but were not located in quadrats (Table 9). This included four dominant forest eucalypts, a hybrid and a eucalypt taxon (*E. virginia* ms) previously collected in the area (1961) but not recognised as unique until the present study. Many of these locally endemic taxa are also rare (Table 9). A substantial number of collections made during this study require further clarification of taxonomic status. Thus additional taxa may subsequently be found to be restricted to the Tingle Mosaic. The considerable variation within what is currently accepted as a species suggests that several genera require major revision. These include *Hemigenia*, *Astartea*, *Bacckea*, *Agonis*, *Calandrinia*, *Aotus*, *Chorizema*, *Daviesia*, *Jacksonia*, *Latrobea*, *Leucopogon*, *Logania*, *Olearia* and *Hibbertia*.

The distribution of the endemic taxa is not even. For example 29 priority flora are known to occur within 10 km of Mt Lindesay (314 km²) compared with 130 for the whole of the Southern Forest Region (14 400 km²). This is a ratio of 10.2:1 on an area basis.

Many taxa found most commonly in drier or more seasonal environments than the Tingle Mosaic have lim-

ited ranges within the Tingle Mosaic (Table 10). These are usually confined to upland north-east facing slopes (e.g. *Banksia gardneri* var. *brevidentata* in the Soho Hills) or deep sands (e.g. *B. coccinea* in Redmond Forest Block) within the Tingle Mosaic. Many taxa that are confined to high rainfall, less seasonal areas and do not extend into the drier parts of the Tingle Mosaic, have range limits within the area (e.g. *Anthocersis sylvicola*, *Lomandra ordii* and *Reedia spathacea*, the latter being confined to peat swamps west of the Bow River catchment). Other species occurring in peat swamp habitats, such as *Cosmelia rubra* and *Cephalotus follicularis* have distributions centred in the Tingle Mosaic.

Table 9

Taxa endemic to the study area.

Taxon
* <i>Actinotus</i> sp Walpole (J R Wheeler 3786)
* <i>Alexgeorgea ganopoda</i>
* <i>Andersonia</i> aff. <i>setifolia</i> (? <i>A. macronema</i>)
* <i>Andersonia auriculata</i>
* <i>Andersonia</i> sp Collis (G Wardell-Johnson 5 A)
* <i>Andersonia</i> sp Middle Rd. (A R Annels 1059)
* <i>Andersonia</i> sp Mitchell River (B G Hammersley 925)
* <i>Andersonia</i> sp Mt. Lindesay (J A Cochrane 405)
* <i>Anthocersis sylvicola</i> ms. (P G Wilson 6312)
* <i>Boronia virgata</i>
* <i>Borya longiscapa</i>
* <i>Bossiaea webbia</i>
* <i>Caladenia evanescens</i>
* <i>Calothamnus</i> sp Mt. Lindesay (B G Hammersley 439)
* <i>Cryptandra congesta</i>
* <i>Eriochilus scaber</i> subsp <i>orbifolia</i> ms
* <i>Eucalyptus brevistylis</i>
* <i>Eucalyptus ficifolia</i>
* <i>Eucalyptus ficifolia</i> x <i>calophylla</i>
* <i>Eucalyptus guilfoylei</i>
* <i>Eucalyptus jacksonii</i>
* <i>Eucalyptus virginia</i> ms (A R Annels 3107)
* <i>Gastrolobium brotenii</i>
* <i>Grevillea fuscolutea</i>
* <i>Lambertia</i> aff. <i>uniflora</i> (A R Annels 1024)
* <i>Microtis globula</i>
* <i>Rorippa dictyosperma</i> (G J Keighery 11945)
* <i>Sollya drommondii</i>
* <i>Spyridium riparium</i>
* <i>Tetratheca elliptica</i>
* <i>Thelymitra jacksonii</i> ms
* <i>Trymalium venustum</i>
* <i>Verticordia apecta</i>

* priority taxa; * taxa not recorded during this survey.

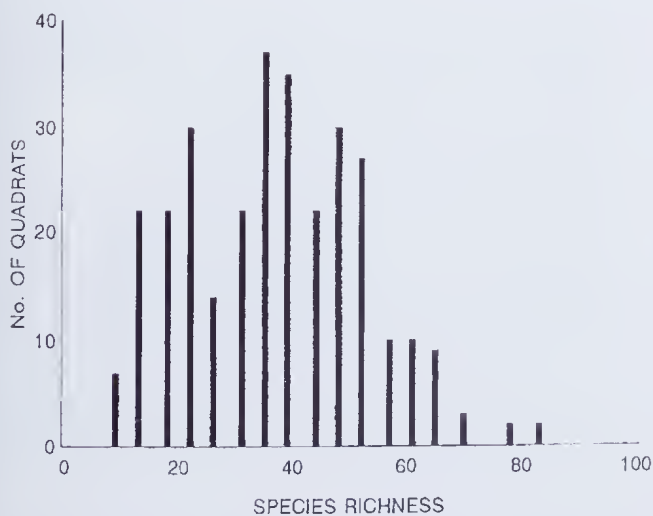


Figure 9. Numbers of quadrats plotted against species richness for 304 quadrats in the Tingle Mosaic.

Table 10

Taxa with ranges ending in the Tingle Mosaic.

Western limit

Acacia biflora
Acacia luteola
Acacia sulcata
Agonis marginata
Banksia coccinea
Banksia gardneri var *gardneri*
Banksia gardneri var *brevidentata*
^{*} *Banksia goodii*
^{*} *Banksia verticillata*
Billardiera sp South Coast (A R Annels 227)
Brachysema sericeum
^{*} *Chorizema reticulatum*
^{*} *Conostylis misera*
Dryandra serra
Eucalyptus angulosa
^{*} *Eucalyptus buprestium*
^{*} *Eucalyptus decurva*
Eucalyptus dorotoxylon
Eucalyptus missilis
Eucalyptus occidentalis
Eucalyptus staeri
Eucalyptus wandoo (SW limit)

Eastern limit

^{*} *Actinotus laxus* ms
Chaetanthus leptocarpoides
Chorizema retrorsum
Eucalyptus calcicola
Galmia sp Yelverton (G J Keighery 10820)
Hemigenia microphylla (SE outliers)
^{*} *Hypocalymma* sp Scott River (A S George 1177)
^{*} *Reedia spathaceae*
^{*} *Hypolaena caespitosa* ms
^{*} *Hypolaena viridis* ms
^{*} *Kennedia glabrata*
^{*} *Lambertia orbifolia*

Southern limits and outliers

^{*} *Chamaelaucium forrestii* subsp *forrestii* ms
^{*} *Darwinia thymoides*
^{*} *Diuris drummondii*

Grevillea umbellulata subsp *acerosa*
Hakea lasiantha
Isopogon latifolius
Lambertia echinata subsp *citrina*
^{*} *Latrobea* sp South Coast (Ashby 1949)
^{*} *Lepidium pseudotasmanicum* (SW limit)
^{*} *Lepyrodia hermaphrodita*
^{*} *Lepyrodia monoica*
^{*} *Lysinema lasianthum*
Melaleuca sp (A R Annels 863)
Melaleuca violacea
Monotoca tamariscina
Nemcia crenulata
^{*} *Platytheca juniperina*
Rinzia schollerifolia
Schoenus trachycarpus
^{**} *Sphenotoma drummondii*
^{*} *Sphenotoma parviflorum*
Synaphea polymorpha
^{*} *Verticordia endlicheriana* var *angustifolia*
^{*} *Verticordia fimbriolepis* subsp *australis*
^{*} *Xanthosia singuliflora*

Lepyrodia extensa ms
^{*} *Lomandra ordii*
^{*} *Melaleuca ringens*
^{*} *Restio jacksonii*
^{*} *Restio ustulatus*
^{*} *Sporodanthus rivularis* ms
Patersonia umbrosa var *xanthina*
Stylidium laciniatum
Stylidium pritzelianum
Taraxis glaucescens ms
Taraxis grossa

^{**} *Drakaea micrantha*
^{**} *Epiblema grandiflorum* var *cyanea* ms
^{*} *Grevillea cirsiifolia*

^{*} priority taxa; ^{**} taxa not recorded during this survey.

Discussion

The Tingle Mosaic includes both great floristic richness and many rare and locally endemic plant species. Detailed taxonomic work on the collections made during this survey is likely to provide further insight into the historical biogeography, and evolutionary history of the area. Other floristic studies of the high rainfall zone (HRZ) in the Swan Coastal Plain and along the south-coast, which have included over 1200 quadrats and 2000 species, demonstrate the individualistic nature of the floristics of the HRZ and that over 25% of the quadrat-based flora records are of taxa recorded only in a single quadrat (Gibson *et al.* 1994; N Gibson, CALM, *pers. comm.* 1995). Although new taxa continue to be discovered in forest sites, these are the least variable of the community types at a landscape scale. Sites in tall-open forest tend to be poorest in species (excepting extreme sites), with least variation across the landscape. The overall floristic diversity of the HRZ is very high. The

richness of the flora of the region is related to this rich landscape pattern, which in turn is associated with a diverse climatic and edaphic history.

Endemism in the Tingle Mosaic

The Tingle Mosaic is notable for high species richness of locally endemic species. Several other south-western areas are also notable for high richness of local endemic and rare species (e.g. Whicher Range, Darling Scarp). However, none are notable for the high numbers of locally endemic dominant species described by this study. For example, five species of dominant forest eucalypts are locally endemic to the Tingle Mosaic. These species were considered by Wardell-Johnson & Coates (1996) to be indicators of a non-mobile, small-scale relictual biota that is confined to the region.

Swamp and outcrop sites are likely to have been important refugia for both the mesic and dry country elements of the biota during the major climate fluctuations

since the mid Tertiary (Hopper 1979; Hopkins *et al.* 1983). Isolation of populations in these sites has led to differentiation and speciation in some woody plant genera (e.g. *Agonis*, *Andersonia*, *Chamaelaucium* and *Leucopogon*). *Eucalyptus brevistylis*, a tall forest tree, is the largest species endemic to granite outcrop sites. This species is also locally endemic to the Tingle Mosaic and associated with the moisture gaining sites at the base of granite outcrops in areas of high relief.

The high levels of endemism associated with upland granite outcrop areas is no doubt associated with the geological and climatic history of the area. Thus sites relatively high in the landscape may have become islands during marine transgressions. Large islands such as Mt Lindesay may have retained a greater array of habitat-types than smaller islands such as Granite Peak, Mt Frankland and Mt Roe. These smaller peaks retain many rare and locally endemic taxa, but only a small proportion of the total within the region in comparison with Mt Lindesay.

Association of floristics with environmental attributes

The Tingle Mosaic features high landscape diversity encompassing hills and ridges, granite monadnocks, swamp, steep river valleys, dune systems and coastal cliffs. This area includes vegetation types ranging from tall open-forests to herblands and includes high levels of heterogeneity immediately adjacent to the forests and woodlands. Thus 36 of the 44 community types are outside the forests. Of these, six are community types occurring on outcrops and 22 occur in swamp habitat. Both these landscape features include high gamma plant diversity.

The degree to which community types are associated with the landform soils units of Churchward *et al.* (1988) is likely to vary between community types. Soil type appears to be stronger than landform in its associations with community types in hill and ridge areas of granitic base rock. However, at a fine-scale, considerable variation has been noted within the community sub-types of the tall open-forests of the area. For example, Inions *et al.* (1990) examined variation in floristics within regenerating karri forest over a major part of the range of karri. They defined 13 community types on the basis of floristic variation, each differing in productivity as measured by age-standardised top-height. This was despite the finding of Wardell-Johnson *et al.* (1989) that karri forest displayed the lowest alpha and gamma diversity of the 12 community types that they defined in the Walpole-Nornalup National Park. Twelve community sub-types are defined within the three community types of the Tall open-forest Communities Supergroup in this study.

The swamps of the area are important features of the landscape and exhibit great variation from peat swamps, estuaries, lakes and playas. This diversity of swampland has been recognised in landform-soils mapping of the south-west. Of the 37 landform-soils units mapped by Churchward *et al.* (1988) along the south coast, 2 are valley units (17 sub-units), and 16 are units in swampy terrain. Thus half of the units identified by Churchward *et al.* (1988) are based on riparian or swampy terrain, although these occupy a minor proportion of the total landscape of the study area. Although the topography is muted, the origin and expression of this variation is not,

and sharp ecotones between communities supergroups are a feature of the Tingle Mosaic (Wardell-Johnson *et al.* 1989).

Floristic pattern in granite outcrop and swamp communities reflects high levels of complexity in landform soils mapping in these environments (Churchward *et al.* 1988). Swamp and outcrop communities have high gamma diversity. An expanded program of survey would be required to target the exceptional variety of environments in the Swamp and outcrop Communities Supergroup. The high water table in areas of swamp vegetation leads to a close link between water table and community structure in an area of great edaphic complexity. These community types are also likely to be most vulnerable to changes in land use.

There is considerably less floristic diversity occurring in tall open-forest than in other vegetational structural types. Two community supergroups (D and E), representing eight community types, occur in hills and plateau landform units and include forest. Open-forest, tall open-forest and woodland communities included most of the quadrats (356 of 441) and also occupied the largest area within the region. Thus hill and plateau units represent over 54% of the total survey area but include few of the community types. The open-forest areas include high levels of α diversity, and occur on shallow and infertile soils of this high rainfall zone.

Integration of floristic classifications and landform soil mapping

There are many site-based floristic studies for, or near, the Tingle Mosaic. Wardell-Johnson *et al.* (1989) developed a floristic classification of the Walpole-Nornalup National Park based on 219 quadrats and 233 species. Inions *et al.* (1990) defined 13 community types on the basis of floristic variation within regenerating karri forest over a major part of the range of karri. Strelein (1988) defined seventeen site types based on the floristic composition of over 400 sites in the southern part of the range of jarrah using the methods of Havel (1968, 1975 a,b). Both Inions *et al.* (1990) and Wardell-Johnson *et al.* (1989) provided a means of allocating independent sites to the classification using discriminant functions on species defined as indicators in the analysis (72 and 52 species respectively). Thus sites in one classification can be defined according to another. Classifications developed in both studies have used similar methods and both schemes can be mapped (Ward & Wardell-Johnson 1993). However, although Hopper *et al.* (1992) concluded that an integration of site-based work (in the Warren Botanical Subdistrict) is desirable, considerable site revisiting would be required. The present study allows the integration of previous studies carried out over a small area, or within a subset of the variation in floristic composition (*i.e.* either in jarrah or karri forest) of the region. This work is required urgently and would allow an environmental context for the management of the region.

Floristic mapping

Previous maps of the floristics of the Tingle Mosaic area include a vegetation map (Smith *et al.* 1991) which recognized the association of the twelve community types defined by Wardell-Johnson *et al.* (1989) with the

landforms/soil units of Churchward *et al.* (1988). Nevertheless, the complexity of the floristics in the Swamp and outcrop Communities Supergroup was underestimated by this work. Ward & Wardell-Johnson (1993) provided a trial mapping of the community types determined by Inions *et al.* (1990) which found that these community types varied in a complex pattern in karri forest. They concluded that while mapping of community types was feasible, it was both expensive and time-consuming. They suggested that resources would be better spent integrating remote sensed imagery with site-based quadrat data to derive models of vegetation communities. The distribution of community types defined by Inions *et al.* (1990) is broadly geographically based (Wardell-Johnson & Christensen 1992), although overlap occurs within a single landform/soils unit (as defined by Churchward *et al.* 1988).

The forests, however, have been mapped at fine scale. The whole of the HRZ (apart from gaps in the Leeuwin Naturaliste Ridge) was vegetation mapped at 1:25 000 scale, from aerial photographs of 1:40 000 scale, during the 1950s and 1960s. A series of 233 maps of the area were produced and the data digitised for the Forest Management Information System (FMIS) as 2 hectare square grid cells. These data were updated, usually using 1:25 000 scale colour aerial photography during the late 1970s. These maps provide the structure, density and floristic composition of the overstorey of all of the south-western forests (excepting that area mentioned above). The Forests Department aerial photography interpretation (API) type-maps used a structural classification system of plant communities which combined height/life form of dominant plants and the projective area of ground covered by the foliage of the dominant plants in the ecosystem. Within these structural subdivisions, species composition of the overstorey was used to define forest type.

There is a need to amalgamate the plant communities defined by this study with those from other studies (*e.g.* Strelein 1988; Wardell-Johnson *et al.* 1989; Inions *et al.* 1990; Gibson *et al.* 1994) and with broad scale vegetation mapping (*e.g.* Beard 1972-80; Smith 1972, Hopkins *et al.* 1995). There is also a need to access existing information in relation to the distribution of forest types particularly that available at 1:25 000 scale API maps prepared during the 1960s. This in conjunction with remote sensed imagery will allow more effective extrapolation of existing quadrat-based data. The continuum of vegetation community types in the Tingle Mosaic requires acknowledgment in vegetation mapping, as with research in the northern jarrah forest by Heddle *et al.* (1980). Thus the landform/soils maps of Churchward *et al.* (1988) should form the basis of maps of complexes of community types in the Tingle Mosaic. The boundaries of these sub-communities are often diffuse. The presentation of summary information of individual community types (and sub-types) and their geographic distribution would be helpful in the mapping of these environments. This would be of considerable benefit to managers of the environment of the Tingle Mosaic.

Hierarchies of mapping units for land resource and vegetation survey allow consistent approaches with mapping scales at varying levels of complexity. Higher levels of complexity of the biota are revealed at finer

scales of mapping. At the local scale, a sound perspective for reserve selection and design, and for ecosystem management is provided by studies covering a broad range of environments and incorporating a thorough assessment of the biota. A hierarchy of mapping units for land resource survey prepared for the Darling District (P Tille, Agriculture WA, *pers. comm.*, 1995) includes the HRZ. Can this approach also be used in reserve system design and management?

A similar hierarchy of vegetation types, based on the structural types of Beard (1980-1981) has been developed for the State of Western Australia (Hopkins *et al.*, *pers. comm.*) using aerial photographic interpretation in combination with detailed field assessment. The digitised vegetation types were digitised from the original line-work and 1: 250 000 scale maps prepared by Beard (1980, 1981). His scheme is based on physiognomy similar to that of Specht (1981), but he classified the vegetation according to the ecologically dominant stratum rather than the tallest stratum. This recognises 823 types, 199 groups and 50 supergroups. The supergroups are used in producing a new 1: 3 000 000 scale map of the vegetation of Western Australia.

Although the difficulty of mapping vegetation communities in topographically subdued landscapes with an apparently homogenous overstorey has been amply demonstrated (Havel 1975a,b), mapping complexes of such communities has become an important tool to determine reservation status and to guide its management (Heddle *et al.* 1980). Structural vegetation types and landform/soils mapping, both derived from the interpretation of remotely sensed imagery (usually aerial photography) are useful tools when used in conjunction with regional floristic survey. The amalgamation of floristic studies from the HRZ will allow a more effective overall hierarchy to be developed of plant community assemblages in the area.

Conclusions

The Tingle Mosaic region had already been noted for its high diversity of herbaceous perennial taxa (Hopper *et al.* 1992), but is also notable for diversity among shrub and tree perennial taxa. This study identified many new taxa, and shows that the area is an important refuge for many high rainfall relictual woody taxa besides the tingle trees after which the area has been designated. The ancient and complex geological history marked by prolonged leaching and erosion, deposition and lateritization of the land-surface has resulted in a subdued landscape despite its complex ontogeny. This varied climatic and edaphic history has no doubt contributed to the present richness of the flora. The present study quantifies this variation for the vascular plants, while Horwitz (1994) demonstrated the high levels of endemism in the freshwater invertebrates of the region. Wardell-Johnson & Horwitz (1996) demonstrated the need for a new approach in fine-scale management in the HRZ to reflect and account for the biotic variation in the region.

This study has provided a means for deriving an understanding of the local scale pattern of the biota in ar-

eas of high biotic richness and high levels of land use pressure. The integration of site-based work, the definition of complexes of community types, and the mapping of these floristic assemblages are applications of this research which would be invaluable in the management for the conservation of biodiversity in the region.

Acknowledgments: We thank T Annels, C Vellios, G Liddelow and I Wheeler for assistance in the field, Y Winchcombe and N Gibson for advice on database management data entry software. M Lyons converted the floristic database to the SEDIT scheme. R Hearn and T Annels contributed the data on endemism and rarity in the region. Many individuals who assisted with the locations of rare taxa or unusual sites in the Tingle Mosaic. These included T Annels, B and G Jackson, A Syme, B Shur, C Chappelle, A Luscombe, B Hammersley and A Wardell-Johnson. Many colleagues are thanked for their identifications in their particular areas of expertise; T MacFarlane, G Keighery, N Gibson, P Wilson, B Rye, B Maslin, A Brown, J Wheeler, H White and R Cranfield from CALM, S Hopper and K Meeney from the Kings Park and Botanic Garden; P Short, Nahonal Botanic Garden, Melbourne; M Crisp, Australian National University; L Craven, CSIRO; K Wilson, Royal Botanical Gardens, Sydney; and A Lowrie, K Lemson, A George and F George. Many volunteers who assisted with locations of rare taxa or unusual sites in the Tingle Mosaic included B Jackson, A Syme, B Shur, B Hammersley and A Wardell-Johnson. We also thank the Walpole-Nornalup National Parks Association and the Walpole District and Southern Region of the Department of Conservation and Land Management for continued support. We thank CALM and the Australian Heritage Commission for support and funding. We also thank the Walpole-Nornalup National Park Association and the Walpole District staff for continued interest in the project, D Bell, D Coates, N Gibson, P Tille, M Churchward, A Hopkins, S Hopper, B Main, B York Main, A Wardell-Johnson and P Withers for constructive comments and for helpful discussion and advice.

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Appendix

List of taxa for the Tingle Mosaic with constancy (percentage of sites occupied by the species) for each taxon of each community group (A1-A4, B1-B2, C1-C3, D1-D2, E1).

Community Group: Number in Group:	A1 64	A2 14	A3 53	A4 10	B1 29	B2 11	C1 14	C2 8	C3 13	D1 71	D2 65	E1 89
Adiantaceae												
<i>Cheilanthes austrotenuifolia</i>			2					25	8	3	2	
Aizoaceae												
<i>Carpobrotus modestus</i>					14							
Amaranthaceae												
<i>Ptilotus stirlingii</i> var <i>laxus</i>					10							
Anthericaceae												
<i>Agrostocrinum scabrum</i>	9		17	10			14		15	6	38	
<i>Borya longiscapa</i>									8			
<i>Borya sphacrocephala</i>								13	8			
<i>Caesia parviflora</i>			9				7	13	23		6	
<i>Chamaecilla corymbosa</i>		7	8		14			50	54	1	6	
<i>Corynotheca micrantha</i> var <i>panda</i>					7							
<i>Johnsonia lupulina</i>	66	14	53			18	14		8		25	
<i>Laxmannia jamesii</i>									8			
<i>Laxmannia minor</i>									23			
<i>Sowerbaea laxiflora</i>				10	55				15		3	
<i>Thysanotus arenarius</i>			2						8	1		
<i>Thysanotus gracilis</i>			4	20	14	9				1	2	
<i>Thysanotus manglesianus</i>			2		7							
<i>Thysanotus multiflorus</i>	42	14	28	20		27	21		31	11	37	2
<i>Thysanotus patersonii</i>										1		
<i>Thysanotus pauciflorus</i>										6	3	
<i>Thysanotus</i> sp											3	
<i>Thysanotus sparteus</i>	2	43	23								6	
<i>Thysanotus tenellus</i>			2								2	
<i>Thysanotus thyrsoides</i>	3								15	6	12	
<i>Tricoryne elatior</i>	5		2						15		2	
<i>Tricoryne humilis</i>				20	14		7		8	1	15	
Apiaceae												
<i>Actinotus glomeratus</i>	14		4			9			8		2	
<i>Actinotus omnifertis</i>	2		11			27						
<i>Apium prostratum</i> var <i>prostratum</i>					3							
<i>Centella asiatica</i>				10								
<i>Daucus glochidiatus</i>							7					
<i>Hydrocotyle callicarpa</i>							7		15			
<i>Hydrocotyle plebeia</i>				30								
<i>Hydrocotyle</i> sp 1									8			
<i>Hydrocotyle tetragonocarpa</i>				20	24							
<i>Pentapeltis silvatica</i>			2							3	32	
<i>Platysace anceps</i>										7		2
<i>Platysace compressa</i>	33		28	10	17			13		35	46	4
<i>Platysace filiformis</i>										8	5	
<i>Platysace pendula</i>	27		8			9					3	
<i>Platysace tenuissima</i>	2											
<i>Trachymene anisocarpa</i>										3		
<i>Trachymene pilosa</i>				30	14				31			
<i>Xanthosia candida</i>			2		3				8	4	6	
<i>Xanthosia fruticulosa</i>									8		2	
<i>Xanthosia hederifolia</i>					3					4	3	1
<i>Xanthosia luegelii</i>	17		11		10					11	32	
<i>Xanthosia rotundifolia</i>	30		30						8	21	48	1
Aspleniaceae												
<i>Asplenium aethiopicum</i>									8			1
<i>Asplenium flabellifolium</i>										1	2	1
Asteraceae												
<i>Asteridea pulverulenta</i>				20	38							
<i>Brachyscome iberidifolia</i>					17		7					
<i>Cotula coronopifolia</i>				10								
<i>Conyza bonariensis</i> *											2	
<i>Craspedia pleiocephala</i>					17			13	23		2	
<i>Gnaphalium sphaericum</i>							7					
<i>Helichrysum cordatum</i>				10	14							1
<i>Helichrysum macranthum</i>					3							
<i>Helichrysum ramosum</i>									15	13	5	27
<i>Hyalosperma cotula</i>									8			
<i>Hypochaeris glabra</i> *		8					7	50	31	10	2	8
<i>Lagenifera luegelii</i>				10	21				15	6	6	
<i>Millotia myosotidifolia</i>				10	14							
<i>Olearia</i> aff <i>paucidentata</i> (GWJ 2959)							7					
<i>Olearia axillaris</i>	2			40	72							
<i>Olearia cassimiae</i>					10			13				
<i>Olearia ciliata</i>				10								
<i>Olearia paucidentata</i>							7			13	3	
<i>Podolepis gracilis</i>					10							
<i>Pseudognaphalium luteoalbum</i> *									8			
<i>Senecio gilbertii</i>			2					13		10	2	2

	A1	A2	A3	A4	B1	B2	C1	C2	C3	D1	D2	E1
<i>Senecio glomeratus</i>							7					
<i>Senecio lautus</i> subsp <i>maritimus</i>				40	79							
<i>Senecio quadridentatus</i>								13				
<i>Senecio ramosissimus</i>				20								3
<i>Siloxerus filifolius</i>			2	10	7			13				
<i>Siloxerus humifusus</i>							14		8			
<i>Sonchus oleraceus</i> *					7			13	8			4
<i>Trichocline spathulata</i>									8			
<i>Vellereophyton dealbatum</i> *										3		
<i>Waitzia citrina</i>				20	48							
Brassicaceae												
<i>Stenopetalum robustum</i>		7			28	9	7					
Campanulaceae												
<i>Wahlenbergia communis</i>								13				
<i>Wahlenbergia gracilentia</i>									1			
Casuarinaceae												
<i>Allocasuarina decussata</i>			8				7			65	15	71
<i>Allocasuarina fraseriana</i>	86		15		7	9			8	1	15	1
<i>Allocasuarina humilis</i>	2			20	21				46		2	
Centrolepidaceae												
<i>Aphelia cyperoides</i>			6				7		15			
<i>Centrolepis aristata</i>			2									
Cephalotaceae												
<i>Cephalotus follicularis</i>						9						
Chenopodiaceae												
<i>Atriplex prostrata</i> *								13				
<i>Rhagodia baccata</i>				20	17							
<i>Sarcocornia quinqueflora</i>							7					
Colchicaceae												
<i>Burchardia monantha</i>							7					
<i>Burchardia multiflora</i>	13		13	10		9		13	31		2	
<i>Burchardia umbellata</i>	45	29	36			9		13			5	
<i>Wurmbea dioica</i> subsp <i>alba</i>								13				
<i>Wurmbea monantha</i>					7							
Convolvulaceae												
<i>Dichondra repens</i>					3							1
Cyperaceae												
<i>Baumea</i> sp (GWJ 5231)						9						
<i>Baumea</i> sp (GWJ 3056)						9						
<i>Baumea juncea</i>						9	14	13				
<i>Baumea vaginalis</i>							7					
<i>Carex</i> sp (GWJ 5229)								13				
<i>Cyathochaeta avenacea</i>	6	14	36			9	36	13	31	11	25	
<i>Cyathochaeta clandestina</i>	8		6								5	
<i>Evandra aristata</i>	3	36	15	10		73					5	
<i>Evandra pauciflora</i>			4									
<i>Gahnia filum</i> ^d					7							3
<i>Gahnia decomposita</i>			4	20		18	57			3	2	
<i>Gymnoschoenus anceps</i>			9			36						
<i>Isolepis marginata</i> *	8			10		9			8			
<i>Isolepis nodosa</i> ¹				30	31		14	13	8			
<i>Isolepis prolifera</i> *								13	8			
<i>Lepidosperma</i> aff <i>gracile</i> (GWJ 5257)									8			
<i>Lepidosperma</i> aff <i>angustatum</i>									8			
<i>Lepidosperma</i> aff <i>tenue</i> (GWJ 5258)											2	
<i>Lepidosperma angustatum</i>	27		15	30	76	18	21	38	77	10	37	3
<i>Lepidosperma effusum</i>			8	40	3			75	15	56	2	87
<i>Lepidosperma gladiatum</i>				60	28							
<i>Lepidosperma gracile</i>				10						1		
<i>Lepidosperma leptostachyum</i>	13	29	8	10	17			25	15	80	65	21
<i>Lepidosperma longitudinale</i>				10				13				
<i>Lepidosperma squamatum</i>	2											
<i>Lepidosperma tenue</i>	3		23		3				15	1	14	
<i>Lepidosperma tetraquetrum</i>								25		3		2
<i>Lepidosperma viscidum</i>					3							
<i>Mesomelaena graciliceps</i>	13		9			9						1
<i>Mesomelaena stygia</i> [*]	11	7	17			18			38		12	
<i>Mesomelaena tetragona</i>	8	14	66				43		46	1	15	
<i>Mesomelaena uncinata</i>									8			
<i>Reedia spathacea</i>							9					
<i>Cyperaceae</i> sp big											2	
<i>Cyperaceae</i> sp fine											2	
<i>Cyperaceae</i> sp l			2						15	1		
<i>Schoenus acuminatus</i>	2											
<i>Schoenus</i> aff <i>rodwayanus</i>	2		2		7	18						
<i>Schoenus bifidus</i> ^b	16		15	20		27				3	15	
<i>Schoenus brevisetis</i> ^a	5					9			15			
<i>Schoenus brevisetis</i> vel sp aff	2	7	4	10	7	9						
<i>Schoenus curoifolius</i>			2									
<i>Schoenus grandiflorus</i>	3		15		24					1	15	
<i>Schoenus odonocarpus</i>							7				5	

	A1	A2	A3	A4	B1	B2	C1	C2	C3	D1	D2	E1
<i>Schoenus subulbosus</i>	2		13							1		
<i>Schoenus subflavus</i> ^c	13					9			8	1		
<i>Tetraria octandra</i>										3	8	
<i>Tricostularia neesii</i> var <i>elatio</i> r			6								2	
<i>Tricostularia neesii</i>	6		2		3	9					5	
Dasypogonaceae												
<i>Baxteria australis</i>	2		8			9						
<i>Calectasia grandiflora</i>									23			
<i>Chamaeceros</i> sp nov								13				
<i>Dasypogon bromeliifolius</i>	100	57	66		3	45					5	1
<i>Kingia australis</i>	5	36	47				7			7	31	
<i>Lomandra caespitosa</i>	2		4		3					1	2	
<i>Lomandra drummondii</i>	20		30			9			8	27	46	3
<i>Lomandra hermaphrodita</i>	2								8		2	
<i>Lomandra integra</i>	9		8							34	34	6
<i>Lomandra micrantha</i>											2	
<i>Lomandra nigricans</i>	28		25			9				17	8	11
<i>Lomandra pauciflora</i>	5		25	10			14	25		83	55	7
<i>Lomandra preissii</i>											3	
<i>Lomandra purpurea</i>	2		8								3	
<i>Lomandra sericea</i>	5		8						38		31	
<i>Lomandra sonderi</i>	2										2	
Dennstaedtiaceae												
<i>Pteridium esculentum</i>	6	29	15			18		38		92	20	75
Dilleniaceae												
<i>Hibbertia</i> sp (GWJ 4822)									8			
<i>Hibbertia</i> aff <i>pulchra</i> (GWJ 4183)	20		6				7		54		5	
<i>Hibbertia amplexicaulis</i>	13		28	20	17		14	13	31	65	74	
<i>Hibbertia commutata</i>	11		4		7			13	15	28	55	3
<i>Hibbertia cuneiformis</i>			4	20	62					4	2	16
<i>Hibbertia cumminghamii</i>			9	20	10		21	13		4	20	2
<i>Hibbertia desmophylla</i>	6											
<i>Hibbertia furfuracea</i>	20	7	8	10	7					27	6	35
<i>Hibbertia glaberrima</i>	5			10	3							
<i>Hibbertia grossulariifolia</i>				20	55							
<i>Hibbertia hypericoides</i>	16		2		3	9						
<i>Hibbertia inconspicua</i>										3		
<i>Hibbertia microphylla</i>									15			
<i>Hibbertia racemosa</i>	2				21							
<i>Hibbertia serrata</i>										21	3	42
<i>Hibbertia silvestris</i>									8	1	5	
<i>Hibbertia stellaris</i>			2				21					
Droseraceae												
<i>Drosera</i> sp (climber)			2			9			15	1	3	1
<i>Drosera erythrorhiza</i>				10	7		7		15			
<i>Drosera glanduligera</i>			2			9				3		
<i>Drosera hamiltonii</i>						9						
<i>Drosera huegelii</i>	2		4					13	8	1	2	
<i>Drosera macrantha</i> subsp <i>macrantha</i>			2									
<i>Drosera menziesii</i>	2	14	13			45	14	13	38	1	2	
<i>Drosera neesii</i>	5		13				7					
<i>Drosera pallida</i>	30	79	42		21	18		25	23	23	38	1
<i>Drosera pulchell</i>											2	
<i>Drosera</i> sp (rosette)	8		9			18			15		3	
<i>Drosera stolonifera</i> subsp <i>stolonifera</i>						9						
Epacridaceae												
<i>Andersonia</i> aff <i>caerulea</i> (GWJ 1563)	5					9						
<i>Andersonia auriculata</i>	23		6			9						
<i>Andersonia caerulea</i>	44	50	32	10		18			8		15	
<i>Andersonia lehmanniana</i>												
subsp <i>lehmanniana</i>			2									
<i>Andersonia micrantha</i>			2			9						
<i>Andersonia sprengelioides</i>	6				7			38	54		2	
<i>Astroloma baxteri</i>	3											
<i>Astroloma ciliatum</i>									8		2	
<i>Astroloma drummondii</i>	5		4							1	8	
<i>Astroloma epacridis</i>	3										5	
<i>Astroloma pallidum</i>					3				54	1	20	
<i>Brachyloma preissii</i>	13				34		7	13			6	
<i>Cosmolia rubra</i>						27						
<i>Leucopogon</i> sp (GWJ 4828)									15			
<i>Leucopogon alteruifolius</i>						9						
<i>Leucopogon australis</i>	16	36	58		17	64	36		31	15	35	
<i>Leucopogon capitellatus</i>	22	14	21	30	69	9	14	38	38	62	63	15
<i>Leucopogon concinnus</i>			2							1	2	
<i>Leucopogon distans</i>	28						7					
<i>Leucopogon gilbertii</i>	2		4				7					
<i>Leucopogon glabellus</i>	44		8			18			23		12	
<i>Leucopogon gracilis</i>	2											
<i>Leucopogon obovatus</i>	16	29	11							4	6	1
<i>Leucopogon parviflorus</i>	8		4		59	18						

	A1	A2	A3	A4	B1	B2	C1	C2	C3	D1	D2	E1
<i>Leucopogon pendulus</i>	2		4									
<i>Leucopogon polystachyus</i>						18						
<i>Leucopogon propinquus</i>	22		36		14		7	13		20	25	1
<i>Leucopogon pulchellus</i>	2											
<i>Leucopogon reflexus</i>			2				7		15			
<i>Leucopogon unilateralis</i>	13		19		10	18	7	25	23	8	32	
<i>Leucopogon verticillatus</i>	11		21				7		8	92	86	80
<i>Lysinema ciliatum</i>	5		2	10	31	9						
<i>Lysinema conspicuum</i>	2		13						8			
<i>Monotoca tamariscina</i>	11	29	25							10	5	3
<i>Sphenotoma capitatum</i>											2	
<i>Sphenotoma gracile</i>	6	29	43	30		82			15		8	
<i>Sphenotoma squarrosus</i>			2			9						
<i>Styphelia tenuiflora</i>											20	
Euphorbiaceae												
<i>Amperea ericoides</i>	13		8		17					7	9	2
<i>Amperea simulans</i>	11		2									
<i>Amperea protensa</i>			2									
<i>Amperea volubilis</i>				10		18						
<i>Phyllanthus calycinus</i>				10	38			13				
<i>Poranthera aff huegelii</i> (GWJ 2837)											2	
<i>Poranthera huegelii</i>	6		4							7	34	
<i>Ricinocarpos glaucus</i>								13		1		2
Gentianaceae												
<i>Centaurium erythraea</i>	2						7	13				2
Geraniaceae												
<i>Geranium solanderi</i>					28							
<i>Pelargonium australe</i>								13	8			
<i>Pelargonium capitatum</i>			2									
<i>Pelargonium littorale</i>					21							
Goodeniaceae												
<i>Dampiera alata</i>			2						31		8	
<i>Dampiera hederacea</i>	2	14	15			9		13		70	9	58
<i>Dampiera linearis</i>	92	93	83	60		64	71		31	17	54	3
<i>Dampiera trigona</i>							7					
<i>Diaspasis filifolia</i>			8	10		27					2	
<i>Goodenia caerulea</i>									8			
<i>Goodenia catoniana</i>	2		21				14			6	42	
<i>Goodenia filiformis</i> var <i>filiformis</i>							7					
<i>Goodenia leptoclada</i>			9									
<i>Goodenia tenella</i>		7	9									
<i>Lechenaultia expansa</i>	5		11	10	3							
<i>Scaevola crassifolia</i>					24							
<i>Scaevola globulifera</i>					3	9				1		
<i>Scaevola microphylla</i>	2		2			9				25	6	38
<i>Scaevola striata</i>	84		66	10	3	18	7	25	23	25	55	1
<i>Scaevola thesioides</i>									8			
<i>Velleia macrophylla</i>				10								
<i>Velleia trinervis</i>	2		4	40	28	9	21		23			
Gyrostemonaceae												
<i>Gyrostemon sheathii</i>					3							
Haemodoraceae												
<i>Anigozanthos flavidus</i>	14		8	80				13		34	9	21
<i>Conostylis aculeata</i> subsp <i>aculeata</i>			6	20	83		14			3	6	
<i>Conostylis setigera</i>	27		9								12	
<i>Haemodorum laxum</i>	2		2	20		9	21		8	3	3	
<i>Haemodorum paniculatum</i>											2	
<i>Haemodorum spicatum</i>	31	79	19		3	18			8	1	2	
<i>Phlebocarya ciliata</i>	23		2								3	
<i>Tribonanthes australis</i>							7					
Haloragaceae												
<i>Glischrocaryon aureum</i> var <i>aureum</i>									8			
<i>Gonocarpus benthamii</i>										18	8	
<i>Gonocarpus diffusus</i>												
<i>Gonocarpus paniculatus</i>							7					
<i>Gonocarpus simplex</i>			2									
<i>Haloragis brownii</i>				20								
<i>Haloragodendron racemosum</i>												3
Iridaceae												
<i>Gladiolus undulatus</i>							7					
<i>Orthrosanthus laxus</i> var <i>laxus</i>					3							
<i>Patersonia habianoides</i>										3	25	
<i>Patersonia occidentalis</i>	2		21	60	34	9	43	13	38		6	
<i>Patersonia pygmaea</i>									38		2	
<i>Patersonia umbrosa</i> var <i>umbrosa</i>	33	14	26		3		7			35	38	4
<i>Patersonia umbrosa</i> var <i>xanthina</i>										10	15	
<i>Romulea rosea</i>					3				8			
Juncaceae												
<i>Juncus kraussii</i> subsp <i>australiensis</i>							7					
<i>Juncus kraussii</i>				10								
<i>Juncus pallidus</i>					3				8			

	A1	A2	A3	A4	B1	B2	C1	C2	C3	D1	D2	E1
<i>Juncus pauciflorus</i>				10								
<i>Juncus planifolius</i>	2		2				21					
Lamiaceae												
<i>Hemigenia</i> sp (GWJ 4119)	2		2						8	3	8	
<i>Hemigenia</i> sp (GWJ 4517)											2	
<i>Hemigenia microphylla</i>									8			
Lauraceae												
<i>Cassytha capillaris</i>				10								
<i>Cassytha micrantha</i>	16	29	23		3	36	7		8		2	1
<i>Cassytha racemosa</i> ^h	47	29	26	30	21	55	50	13	15	55	54	16
Lentibulariaceae												
<i>Utricularia menziesii</i>								13				
<i>Utricularia multifida</i>			2			9	21					
<i>Utricularia simplex</i>		7										
<i>Utricularia tenella</i>						9	29		31			
<i>Utricularia violacea</i>							7					
Lindsaeaceae												
<i>Lindsaea linearis</i>	58	36	75						15	35	49	
Lobeliaceae												
<i>Isotoma hypocrateriformis</i>	2		2	10	7		7		8		2	
<i>Lobelia alata</i>				80	7		14	13				
<i>Lobelia gibbosa</i>	2		2	10	3							
<i>Lobelia heterophylla</i>			2		41						2	
<i>Lobelia rarifolia</i>		7		10								
<i>Lobelia rhombifolia</i>					3							
<i>Lobelia tenuior</i>	3			50	79							
Loganiaceae												
<i>Logania aff serpyllifolia</i> (GWJ 2743)	2							13	8	4	9	
<i>Logania campanulata</i>									8		5	
<i>Logania serpyllifolia</i>	20		11	30	28		7		15	23	63	1
<i>Logania vaginalis</i>				10	21					3		1
<i>Mitrasacme paradoxa</i>		29	8				7		23	1		
Loranthaceae												
<i>Nyctsia floribunda</i>	8		11				7				3	
Menyanthaceae												
<i>Villarsia lasiosperma</i>				10								
<i>Villarsia parnassifolia</i>				70			43		8			
Mimosaceae												
<i>Acacia aff pentadenia</i> (GWJ 3700)	5		8							7	31	
<i>Acacia alata</i>			2							3	2	1
<i>Acacia biflora</i>	2										2	
<i>Acacia browniana</i>			21				7		38		26	
<i>Acacia cochlearis</i>					21				8			
<i>Acacia crispula</i>			2				14		23			
<i>Acacia divergens</i>	5	7	15	10			21			32	17	2
<i>Acacia extensa</i>	2		2						8		18	
<i>Acacia hastulata</i>												
<i>Acacia littorea</i>				50	55							
<i>Acacia luteola</i>	5		6								6	
<i>Acacia myrtifolia</i>	33		19			9	14	50	8	13	28	1
<i>Acacia nervosa</i>									15			
<i>Acacia pentadenia</i>			11				7	13	15	77	31	97
<i>Acacia pulchella</i>	14		6	40	17		29	25	54	1	14	
<i>Acacia scapelliformis</i>												
<i>Acacia stenoptera</i>			2				36		54		2	
<i>Acacia sulcata</i>									15			
<i>Acacia triptycha</i>									15			
<i>Acacia uliginosa</i>						27						
<i>Acacia urophylla</i>										8		9
<i>Acacia varia</i> var <i>varia</i> ms									8		5	
<i>Acacia willdenowiana</i>											2	
<i>Para-serianthes lophantha</i>									8			
Myoporaceae												
<i>Myoporum oppositifolium</i>			20									
<i>Myoporum tetrandrum</i>			10				7					
Myrtaceae												
<i>Agonis</i> sp (GWJ 2113)	2											
<i>Agonis</i> sp (GWJ 4768)						9						
<i>Agonis</i> sp (GWJ 1953)	3											
<i>Agonis aff juniperina</i> (GWJ 3628)						18						
<i>Agonis flexuosa</i>	22		4	70	83	9	7	25		13		15
<i>Agonis hypericifolia</i>	69		47						38	4	75	
<i>Agonis juniperina</i>		14		10		18						1
<i>Agonis linearifolia</i>			4			64	43	38	31	6		
<i>Agonis marginata</i>								13			2	
<i>Agonis parvicaps</i>	88	86	98			73	14	13	23	42	68	
<i>Astartea fascicularis</i>	3	14	15	10		55	50	13	31			
<i>Baeckea aff crispiflora</i> (GWJ 4827)									8			
<i>Baeckea aff preissii</i> (GWJ 4804)							7					
<i>Baeckea astarteoides</i>							14					
<i>Baeckea camphorosmae</i>			2			9			23			

	A1	A2	A3	A4	B1	B2	C1	C2	C3	D1	D2	E1
<i>Beaufortia decussata</i>	31	21	49								9	
<i>Beaufortia sparsa</i>	5	21	15			82					2	
<i>Calytrix acutifolia</i>					3							
<i>Calytrix asperula</i>	2											
<i>Callistemon speciosus</i>			4			18						
<i>Calothamnus gracilis</i>							7		8			
<i>Calothamnus lateralis</i>			8			9	21		8			
<i>Chamelaucium</i> sp (GWJ 3784)								13				
<i>Conothamnus neglectus</i>			2									
<i>Darwinia citriodora</i>									8			
<i>Darwinia oederoides</i>	3		4						23			
<i>Darwinia vestita</i>	11		4						31			
<i>Eucalyptus angulosa</i>				10	7							
<i>Eucalyptus anceps</i>									8			
<i>Eucalyptus brevistylis</i>										25		7
<i>Eucalyptus calcicola</i>					7							
<i>Eucalyptus calophylla</i>	17		53				7	38	46	85	100	18
<i>Eucalyptus cornuta</i>				20	7			25			2	
<i>Eucalyptus calophylla</i> x <i>ficifolia</i>	13		8							1		
<i>Eucalyptus missilis</i>					7							
<i>Eucalyptus decipiens</i>			2						23			
<i>Eucalyptus diversicolor</i>			4									
<i>Eucalyptus doratoxylon</i>			2					13		55	3	75
<i>Eucalyptus ficifolia</i>	30		9			18				1		
<i>Eucalyptus guilfoylei</i>			8					13		51	11	48
<i>Eucalyptus jacksonii</i>			4							4		47
<i>Eucalyptus marginata</i>	77	79	89			18	14	13	38	46	100	1
<i>Eucalyptus megacarpa</i>	6	7	4	20				13		8	3	
<i>Eucalyptus occidentalis</i>							7					
<i>Eucalyptus patens</i>	6	14	2			18	36	13	23	1		
<i>Eucalyptus rudis</i>											1	
<i>Eucalyptus staeri</i>	16											
<i>Eucalyptus virginia</i> ms											6	
<i>Eucalyptus wandoo</i>									23			
<i>Homalospermum firmum</i>			2			100						
<i>Hypocalymma angustifolium</i>	2		8				7	13	46		9	
<i>Hypocalymma cordifolium</i>							14					
<i>Hypocalymma strictum</i>	50	21	2			9						
<i>Kunzea aff micrantha</i>							7		8			
<i>Kunzea ericifolia</i>						9	7					
<i>Kunzea recurea</i>	17	71	4	20	17							
<i>Kunzea sulphurea</i>	19	7	6			18			8			
<i>Melaleuca acerosa</i>				10	17		7					
<i>Melaleuca aff polygaloides</i> (GWJ 269)								7				
<i>Melaleuca baxteri</i>	2							13				
<i>Melaleuca cuticularis</i>				10			43					
<i>Melaleuca densa</i>			2				79					
<i>Melaleuca diosmifolia</i>					7			13				
<i>Melaleuca incana</i>					7							
<i>Melaleuca microphylla</i>						9		13		4		
<i>Melaleuca pauciflora</i>						9	21					
<i>Melaleuca polygaloides</i>					3							
<i>Melaleuca preissiana</i>	2		8			36	14		8			
<i>Melaleuca raphiophylla</i>							14	25	8			
<i>Melaleuca scabra</i>									8			
<i>Melaleuca spathulata</i>							14					
<i>Melaleuca thymoides</i>	83		8		21	18			8		2	
<i>Melaleuca violacea</i>							7					
<i>Pericalymma crassipes</i>			15				29		8			
<i>Pericalymma ellipticum</i>											1	11
<i>Rinzia scholleriifolia</i>	6								8			
<i>Scholtzia</i> sp torn												2
<i>Verticordia</i> sp (GWJ 4830)									8			
<i>Verticordia habrantha</i>									23			
<i>Verticordia plumosa</i>								13	31			
Olacaceae												
<i>Olax benthamiana</i>	2											
<i>Olax phyllanthi</i>	11		6	60	21	9	7		8		3	
Orchidaceae												
<i>Burnettia forrestii</i>											2	
<i>Burnettia nigricans</i>					3						2	
<i>Caladenia aphylla</i>	6	7										
<i>Caladenia corynephora</i>												1
<i>Caladenia flava</i>	6	14	4		10			13	23	13	17	1
<i>Caladenia huegelii</i>									15	1	3	
<i>Caladenia interjacens</i>					7							
<i>Caladenia latifolia</i>					28			13		1	3	2
<i>Caladenia longiclavata</i> var <i>longiclavata</i>											2	
<i>Caladenia marginata</i>								13				
<i>Caladenia pectinata</i>											2	
<i>Caladenia nana</i>											2	

	A1	A2	A3	A4	B1	B2	C1	C2	C3	D1	D2	E1
<i>Caladenia sericea</i>			2									
<i>Caladenia</i> sp 1	2									8	5	
<i>Corybas abditus</i>						9						
<i>Corybas recurvus</i>										14	6	7
<i>Cryptostylis ovata</i>	2		2	10	10			13			2	3
<i>Cyrtostylis luegelii</i>					3			13		3		
<i>Cyrtostylis robusta</i>												
<i>Diuris pauciflora</i>				20				13				
<i>Diuris laevis</i>												
<i>Diuris longifolia</i>	3			10	7					1	3	
<i>Drakaea elastica</i>		14										
<i>Drakaea glyptodon</i>	2	7										
<i>Elythranthera braunonis</i>	2		4	10	14	9	7	13	38	1		
<i>Elythranthera emarginata</i>		7			3						3	
<i>Eriochilus dilatatus</i>	3		11		34					6	3	1
<i>Eriochilus pulchellus</i>								25				
<i>Eriochilus scaber</i>		7	15							1		
<i>Gastrodia lacista</i>	3									10		4
<i>Leporella fimbriata</i>			4									
<i>Leptoceras muenziesii</i>												1
<i>Lyperanthus serratus</i>	5								8		5	
<i>Microtis alba</i>												
<i>Microtis media subsp media</i>			2				7					
<i>Microtis</i> sp											2	
<i>Microtis unifolia</i>			4	10			21	25	8			2
<i>Monadenia bracteata</i>			4					13	15			
<i>Paracaleana nigrita</i>	3											
<i>Prasophyllum broomei</i>										7	5	
<i>Prasophyllum drummondii</i>		7				9	7					
<i>Prasophyllum elatum</i>		7										
<i>Prasophyllum fimbria</i>		21	4									
<i>Prasophyllum gibbosum</i>		7							8			
<i>Prasophyllum hians</i>		7										
<i>Prasophyllum odoratum</i>		21										
<i>Prasophyllum parvifolium</i>			2	10					8			
<i>Prasophyllum regium</i>							7					
<i>Pterostylis aff nana</i>											2	
<i>Pterostylis barbata</i>	2		2					13				2
<i>Pterostylis nana</i>					7			25	8	11	6	1
<i>Pterostylis plumosa</i>									8		2	
<i>Pterostylis recurva</i>			2					13		1	9	
<i>Pterostylis scabra</i>					3							
<i>Pterostylis vittata var vittata</i>	3		2		7	9		13	8	10	11	2
<i>Thelymitra antennifera</i>			2					25	31	1		
<i>Thelymitra benthamiana</i>										1	2	
<i>Thelymitra crinita</i>	5	7							38	3	14	
<i>Thelymitra nuda</i>	14		6						15	4	11	
<i>Thelymitra pauciflora</i>	6	14	4	20	7	9			8	1	9	
<i>Thelymitra</i> sp 2			2									
<i>Thelymitra</i> sp 3			2							1	3	
Orobanchaceae												
<i>Orobancha minor</i>					3						2	
Oxalidaceae												
<i>Oxalis purpurea</i>									8			
<i>Oxalis corniculata</i>					3			13				
Papilionaceae												
<i>Aotus genistoides</i>	2	14	4			27	7					
<i>Aotus intermedius</i>						27						
<i>Bossiaea disticha</i>										1	3	
<i>Bossiaea eriocarpa</i>										10	11	
<i>Bossiaea linophylla</i>	13		4	30	38			13		11	35	
<i>Bossiaea oriata</i>			2						23	4	51	
<i>Bossiaea rufa</i>	63	14	15		3	9			8	1	9	
<i>Bossiaea webbii</i>	3		32							24	9	8
<i>Brachysema minor</i>							7				2	
<i>Brachysema sericeum</i>			2				36					
<i>Burtonia conferta</i>	55	71	23	10		18	7		8		14	
<i>Burtonia scabra</i>	9											
<i>Burtonia villosa</i>	5											
<i>Chorizema aciculare</i>									8			
<i>Chorizema aff aciculare</i> (GWJ 2579)	2		2		3	9						
<i>Chorizema diversifolium</i>	2		2	10	28							6
<i>Chorizema ilicifolium</i>					21	9						
<i>Chorizema nanum</i>			4									
<i>Chorizema retrorsum</i>			2							58	22	61
<i>Chorizema rhombeum</i>	2		8							6	5	
<i>Daviesia aff incrassata</i> (GWJ 4526)												2
<i>Daviesia cordata</i>									23	1	12	
<i>Daviesia decurrens</i>	44		4			9			8		2	
<i>Daviesia horrida</i>									38		3	
<i>Daviesia incrassata</i>	2		6								6	

	A1	A2	A3	A4	B1	B2	C1	C2	C3	D1	D2	E1
<i>Daviesia oppositifolia</i>									8			
<i>Daviesia polyphylla</i>											2	
<i>Daviesia preissii</i>	8		6						15		14	
<i>Dillwynia</i> sp. A									38			
<i>Euchilopsis linearis</i>	2											
<i>Eutaxia densifolia</i>			8							6	6	
<i>Eutaxia obovata</i>			30		7			38		3	3	1
<i>Eutaxia parvifolia</i>	2											
<i>Eutaxia virgata</i>							14					
<i>Gastrolobium bilobum</i>			2					25				
<i>Gastrolobium brownii</i>									15	4	5	
<i>Gastrolobium forrestii</i>			2				7			3	2	
<i>Gompholobium aristatum</i>	2											
<i>Gompholobium burtonioides</i>	3						7					
<i>Gompholobium capitatum</i>	34		9								2	
<i>Gompholobium knightianum</i>	6		4						8		12	
<i>Gompholobium ovatum</i>	3		17						15	1	58	
<i>Gompholobium polymorphum</i>			2				7	13	38	3	26	
<i>Gompholobium preissii</i>											2	
<i>Gompholobium tomentosum</i>	2		2	10	21					1	3	
<i>Gompholobium venustum</i>									15		2	
<i>Hardenbergia comptoniana</i>			6	20	24			13		1		6
<i>Hovea chorizemifolia</i>	5		28						23	7	71	
<i>Hovea elliptica</i>	5		15							69	69	19
<i>Hovea trisperma</i>			11				7		8		5	
<i>Isotropis cuneifolia</i>	2				55							
<i>Jacksonia</i> aff. <i>furcellata</i> (GWJ 1411)	16		2	10	48	9						
<i>Jacksonia furcellata</i>	11			10								
<i>Jacksonia horrida</i>	2											
<i>Jacksonia spinosa</i>	2											
<i>Kennedia coccinea</i>	8		19		7					14	29	3
<i>Kennedia microphylla</i>									8			
<i>Latrobea genistoides</i>	14											
<i>Latrobea tenella</i> var. <i>tenella</i>	2		2									
<i>Lotus suaveolens</i> *			2								2	
<i>Lotus uliginosus</i> *			2						15			
<i>Mirbelia dilatata</i>								13	8		9	
<i>Nemcia crenulata</i>									23			
<i>Oxylobium lanceolatum</i>				20		9	7	38	8			1
<i>Phyllota barbata</i>	6											
<i>Pultenaea</i> aff. <i>obcordata</i>					3							
<i>Pultenaea barbata</i>	2											
<i>Pultenaea ericifolia</i>									15		2	
<i>Pultenaea reticulata</i>	77	79	25	30		55				6	2	
<i>Pultenaea strobilifera</i>											2	
<i>Sphaerolobium alatum</i>	2		8							1	14	
<i>Sphaerolobium grandiflorum</i>	3	14	8				7		8	1		
<i>Sphaerolobium macranthum</i>	3		21	20		55	21	13	23		2	
<i>Sphaerolobium medium</i>	5		19				7		8	14	62	
<i>Sphaerolobium nudiflorum</i>											2	
<i>Sphaerolobium racemosum</i>	2			20		9	14				2	
<i>Sphaerolobium vimineum</i>									8			
<i>Templetonia retusa</i>					3							
<i>Trifolium dubium</i> *			2						8			
<i>Viminaria juncea</i>			2									
Philydraceae							43	13	15			
<i>Philydrella pygmaea</i>							21		46			
Phormiaceae												
<i>Dianella revoluta</i>					3		7					
<i>Stypandra glauca</i>								25	8			
Pittosporaceae												
<i>Billardiera coeruleo-punctata</i>			2							1	5	
<i>Billardiera floribunda</i>	2		2						15	14	26	
<i>Billardiera variifolia</i>	23		49			9	7	25	23	87	71	83
<i>Sollya heterophylla</i>	2		2	10	17		14	13	8	1		
Poaceae												
<i>Agrostis avenacea</i>				10			14		8			
<i>Aira caryophyllea</i> *			4				7		38			1
<i>Amphipogon amphipogonoides</i>	2		11			9	14		46	8	28	
<i>Amphipogon avenaceus</i>									8			
<i>Amphipogon debilis</i>			2								2	
<i>Amphipogon laguroides</i>			2								2	
<i>Amphipogon turbinatus</i>	2		4		3	18	7		8	11	9	2
<i>Briza maxima</i> *								13	8			
<i>Briza minor</i> *			4					13	15			
<i>Bromus hordeaceus</i> *											2	
<i>Danthonia caespitosa</i>			2	10	10			38	46		2	
<i>Dichelachne crinita</i>					31							
<i>Echinopogon ovatus</i>			4									1
<i>Festuca littoralis</i>					3		7					
<i>Grass</i> sp. 1									8			

	A1	A2	A3	A4	B1	B2	C1	C2	C3	D1	D2	E1
Grass sp 2									8			
<i>Holcus lanatus</i> *	2		4			9	7			1	2	
<i>Lolium perenne</i> *	2		2				7					
<i>Microlaena stipoides</i>			2		17			13		6	2	1
<i>Neurachne alopecuroides</i>									8			
<i>Poa drummondiana</i>					31		7					1
<i>Poa poliformis</i>			2					13		3		2
<i>Poa porphyroclados</i>				30	28		7					
<i>Poa serpentina</i>							7	13				
<i>Poa</i> sp				10								
<i>Polypogon monspeliensis</i> *								13				
<i>Stipa compressa</i>					10			13			2	
<i>Stipa flavescentis</i>					28							
<i>Stipa tenuifolia</i>			2		3							
<i>Stipa semibarbata</i>									38		2	
<i>Stipa</i> sp 1								13	8			
<i>Tetrarrhena laevis</i>			8		3		7	38	23	89	38	85
<i>Vulpia bromoides</i> *			2									
<i>Vulpia myuros</i> *			2									
Podocarpaceae												
<i>Podocarpus drouynianus</i>	27		11			9				58	77	6
Polygalaceae												
<i>Comesperma calymega</i>	36	43	6	10	7					8	9	
<i>Comesperma confertum</i>	33	14	38	20	31	55	43		8	35	60	8
<i>Comesperma flavum</i>	3	21	6		3	9						
<i>Comesperma volubile</i>			4				7		23	3	9	
Polygonaceae												
<i>Muehlenbeckia adpressa</i>				40	24							
<i>Rumex acetosella</i>											2	
<i>Rumex pulcher</i> subsp <i>pulcher</i> *								13				
Portulacaceae												
<i>Calandrinia brevipedata</i>						9						
<i>Calandrinia calyptrata</i>					48							
Primulaceae												
<i>Anagallis arvensis</i> var <i>arvensis</i> *				10	3			25				
<i>Anagallis arvensis</i> var <i>caerulea</i> *									8			
<i>Samolus junceus</i>				20	10		7					
<i>Samolus repens</i>				10	3							
Proteaceae												
<i>Adenanthos cuneatus</i>	33		2	20		9						
<i>Adenanthos obovatus</i>	83	57	58	40	3	73	7				5	
<i>Banksia attenuata</i>	36				10							
<i>Banksia coccinea</i>	2											
<i>Banksia gardneri</i> var <i>brevidentata</i>	2		2								2	
<i>Banksia gardneri</i> var <i>gardneri</i>											2	
<i>Banksia goodii</i>	2											
<i>Banksia grandis</i>	19		36		31	9	7			38	68	1
<i>Banksia ilicifolia</i>	33											
<i>Banksia littoralis</i>			8	40	7	18	14			3	2	
<i>Banksia occidentalis</i> subsp <i>occidentalis</i>						9	7					
<i>Banksia quercifolia</i>	36		9	20		45	7					
<i>Banksia seminuda</i>							7			1		
<i>Banksia splaerocarpa</i>			2								2	
<i>Banksia verticillata</i>								13				
<i>Conospermum caeruleum</i>	27		9								12	
<i>Conospermum capitatum</i>	5		2								3	
<i>Conospermum flexuosum</i>			2							1	3	
<i>Dryandra armata</i>			2						23		3	
<i>Dryandra formosa</i>										4	9	
<i>Dryandra nivea</i>			8						62		14	
<i>Dryandra serra</i>											5	
<i>Dryandra sessilis</i>					28							
<i>Franklandia fuscifolia</i>	2											
<i>Grevillea acerosa</i>									8			
<i>Grevillea aff manglesioides</i>							7					
<i>Grevillea brontwynae</i>											2	
<i>Grevillea brotenii</i>			2						23		6	
<i>Grevillea circsifolia</i>									15			
<i>Grevillea diversifolia</i> subsp <i>subterseri</i>			2				21					
<i>Grevillea fuscolutea</i>									8			
<i>Grevillea occidentalis</i>			6							3	26	
<i>Grevillea pulchella</i>										11	28	
<i>Grevillea quercifolia</i>			4						8		11	
<i>Grevillea trifida</i>	2		8				14		15	3	28	
<i>Hakea amplexicaulis</i>	2		21						15	35	66	
<i>Hakea ceratophylla</i>	6	7	36	10			29					
<i>Hakea corymbosa</i>									8			
<i>Hakea falcata</i>			9				21		15		11	
<i>Hakea falcata</i> short leaved form											2	
<i>Hakea florida</i>	2		15					25	8	1	17	

	A1	A2	A3	A4	B1	B2	C1	C2	C3	D1	D2	E1
<i>Hakea lasianthoides</i>										10	22	
<i>Hakea lasiantha</i>											2	
<i>Hakea linearis</i>			2	50		9	7					
<i>Hakea lissocarpa</i>									15			
<i>Hakea oleifolia</i>			4	30	45			13		1	5	1
<i>Hakea prostrata</i>					72							
<i>Hakea ruscifolia</i>			4	10			7				15	
<i>Hakea</i> sp 1	2		2									
<i>Hakea trifurcata</i>									8			
<i>Hakea undulata</i>									38	1	3	
<i>Hakea varia</i>	2		4	10	3	9	57		15		8	
<i>Isopogon attenuatus</i>	9		8	10			14		15		9	
<i>Isopogon axillaris</i>			2	10								
<i>Isopogon formosus</i>	3		6						31		11	
<i>Isopogon latifolius</i>	2											
<i>Isopogon sphaerocephalus</i>	3		6								35	
<i>Isopogon teretifolius</i>									8			
<i>Lambertia echinata</i>	2											
<i>Lambertia uniflora</i>											3	
<i>Persoonia aff longifolia</i>	2										2	
<i>Persoonia elliptica</i>										1	11	
<i>Persoonia longifolia</i>	59	71	40			9				70	82	7
<i>Persoonia microcarpa</i>						55						
<i>Petrophile divaricata</i>	5										2	
<i>Petrophile diversifolia</i>			19				21		8	7	46	
<i>Petrophile linearis</i>	3											
<i>Petrophile longifolia</i>	39		4	10					8		2	
<i>Petrophile squamata</i> subsp A			2								2	
<i>Petrophile squamata</i> subsp B							14		8			
<i>Stirlingia tenuifolia</i>							7		8			
<i>Strangetia stenocarpoides</i>	2		26							3	14	
<i>Synaphea petiolaris</i>								13	8		12	
<i>Synaphea polymorpha</i>	2		2									
<i>Synaphea preissii</i>	2										2	
<i>Synaphea reticulata</i>			4						46		5	
Pteridaceae												
<i>Pteris vittata</i>											2	
Ranunculaceae												
<i>Clematis pubescens</i>					10					49	8	58
<i>Ranunculus colonorum</i>								13				
Restionaceae												
<i>Alexgeorgea ganopoda</i>			2			27						
<i>Anarthria gracilis</i>	2	7	9			18						
<i>Anarthria laevis</i>	8		2				21		38			
<i>Anarthria prolifera</i>	97	100	83	30	7	36	21		23	15	66	
<i>Anarthria scabra</i>	95	100	79			36			15	8	17	
<i>Empodisma gracillimum</i>												
<i>Hypolaena exsulca</i>							7					
<i>Hypolaena ramosissima</i>							7					
<i>Leptocarpus</i> sp (GWJ 5249)							7					
<i>Leptocarpus aff tephrius</i> (GWJ 5255)							7					
<i>Leptocarpus diffusus</i>	2					9						
<i>Leptocarpus aristatus</i> ^m	30		15			27	43				5	
<i>Leptocarpus canus</i> ¹			2	10			21	13				
<i>Leptocarpus coangustatus</i>	2			20		18	7					
<i>Lepyrodia drummondiana</i> ¹							7					
<i>Lepyrodia monoica</i>			2									
<i>Sporodanthus strictus</i>	2						14					
<i>Leptocarpus</i> sp 1	3				7				8			
<i>Leptocarpus</i> sp 2	6		2			9	7			1		
<i>Leptocarpus</i> sp 3	2		2				21					
<i>Leptocarpus tenax</i>	39	29	19			55	36				2	
<i>Leptocarpus tenellus</i>							14				2	
<i>Desmodius fasciculatus</i>	20		34				14		85	8	69	
<i>Loxocarya flexuosa</i> ¹	19	7	15	50	97	27	14	25	8	8	31	2
<i>Lyginia barbata</i>	59		11	10	7	18	7		8		2	
<i>Meeboldia denmarkica</i>	2		6				7					
<i>Pseudoloxocarya grossa</i> ms						9						
<i>Restio</i> sp (GWJ 5235)						9						
<i>Restio</i> sp (GWJ 5239)											2	
<i>Restio aff tremulus</i> (GWJ 4534) ¹			4			9	7					
<i>Restio amblycoleus</i>							7					
<i>Restio confertoplicatus</i>	2											
<i>Restio tremulus</i>	5		2				7					
<i>Restio ustulatus</i>	2											
<i>Taraxis glaucescens</i> ms												
Rhamnaceae												
<i>Spyridium globulosum</i>				30	45							
<i>Trymalium floribundum</i>					3			13		17		64
<i>Trymalium venustum</i>					3					3	3	6
<i>Trymalium ledifolium</i> var <i>ledifolium</i>							21		38		8	

	A1	A2	A3	A4	B1	B2	C1	C2	C3	D1	D2	E1
Rosaceae												
<i>Acaena echinata</i> var <i>retrorsumpilosa</i>								13				
Rubiaceae												
<i>Opercularia lispidula</i>	36		25	70	52	18	7	63	23	76	75	16
<i>Opercularia vaginata</i>	2				10		7					
<i>Opercularia volubilis</i>				10			7	13		25		46
Rutaceae												
<i>Boronia crenulata</i> var <i>crenulata</i>	23	36	17	20	3				15	3	12	2
<i>Boronia denticulata</i>							14					
<i>Boronia gracilipes</i>	2		17			9	7	13		80	43	44
<i>Boronia pincea</i>			2				21					
<i>Boronia megastigma</i>						9	21				2	
<i>Boronia molloyae</i>				10				13				
<i>Boronia nematophylla</i>	2											
<i>Boronia virgata</i>		7	2	10								
<i>Boronia spathulata</i>	25		55			18	21		31	1	29	
<i>Boronia stricta</i>		21	2			36		13		1		
<i>Chorilaena quercifolia</i>										8		49
<i>Crocea angustifolia</i> var <i>angustifolia</i>			2								2	
<i>Crocea angustifolia</i> var <i>dentata</i>										56	22	25
<i>Phebalium anceps</i>				40								
Santalaceae												
<i>Exocarpos odoratus</i>					21							
<i>Exocarpos sparteus</i>				10	7							
<i>Leptomeria cunninghamii</i>	14	50	11			18	14	25	8	11	26	1
<i>Leptomeria pauciflora</i>			4				7					
<i>Leptomeria serobiculata</i>	5		2				14			1	2	
<i>Leptomeria squarrosula</i>	2		2								3	
Sapindaceae												
<i>Dodonaea aptera</i>					3			13				
<i>Dodonaea ceratocarpa</i>								13	23			
Saxifragaceae												
<i>Eremosyne pectinata</i>		7										
Scrophulariaceae												
<i>Bellardia trixago</i> *					14			13	8			
<i>Gratiola peruviana</i>				20								
<i>Parentucellia latifolia</i> *									15			
<i>Parentucellia viscosa</i> *				10	14		7					
<i>Veronica distans</i>					3							
<i>Veronica plebeia</i>								13				
Solanaceae												
<i>Anthocercis silvicola</i>												1
<i>Anthocercis viscosa</i>					3							
<i>Solanum nigrum</i> *				10								
Stackhousiaceae												
<i>Stackhousia huegelii</i>										1	5	
<i>Stackhousia monogyna</i>			2		28					3		
<i>Tripterococcus brimontis</i>											3	
Sterculiaceae												
<i>Lasiopetalum cordifolium</i>											5	
<i>Lasiopetalum floribundum</i>			2				7			59	8	70
<i>Lasiopetalum floribundum</i> subsp. nov.											2	
<i>Thomasia foliosa</i>									8			
<i>Thomasia pauciflora</i>							14	50		3		
<i>Thomasia pauciflora</i> var <i>paniculata</i>											2	
<i>Thomasia quercifolia</i>			4							52	6	31
Stylidiaceae												
<i>Levenhookia dubia</i>			2						15			
<i>Levenhookia pusilla</i>	2		2		3		7		31	7	11	
<i>Stylidium</i> sp. (GWJ 3615)						9						
<i>Stylidium adnatum</i>				10						17	5	10
<i>Stylidium</i> aff. <i>luteum</i> (GWJ 2245)							7				2	
<i>Stylidium</i> aff. <i>scandens</i>	2										2	
<i>Stylidium amoenum</i>	5		6			9			8	7	45	
<i>Stylidium assimile</i>						18					2	
<i>Stylidium breviscapum</i>									31		2	
<i>Stylidium brunonianum</i>		7	2								2	
<i>Stylidium caespitosum</i>		7	9				14					
<i>Stylidium calcaratum</i>			2		14	9	14		23	1	2	
<i>Stylidium ciliatum</i>	8		8			18	7					
<i>Stylidium diversifolium</i>	2	21	2			9	21		46			
<i>Stylidium emarginatum</i>		7		20	28				8			
<i>Stylidium fasciculatum</i>					21							
<i>Stylidium galioides</i> *											2	
<i>Stylidium glaucum</i> subsp. <i>angustifolium</i>	3							13				
<i>Stylidium glaucum</i> subsp. <i>glaucum</i>									15			
<i>Stylidium guttatum</i>			2			9						
<i>Stylidium imbricatum</i>			2			9		13				
<i>Stylidium inundatum</i>									8			
<i>Stylidium junceum</i>				50		9					3	
<i>Stylidium laciniatum</i>			2			9						

	A1	A2	A3	A4	B1	B2	C1	C2	C3	D1	D2	E1	
<i>Stylidium lepidum</i>	2												
<i>Stylidium luteum</i>	3		9			9	29		8	7	15		
<i>Stylidium piliferum</i>	8	14	25			9			8	3	9		
<i>Stylidium pritzelianum</i>										10	12		
<i>Stylidium repens</i>	20	43	13	20		9			8		2		
<i>Stylidium rhynchocarpum</i>										41	22	7	
<i>Stylidium scandens</i>	8	43	34		3	18		25	8	4	11		
<i>Stylidium schoenoides</i>	20		8			9			15		6		
<i>Stylidium</i> sp 1											2		
<i>Stylidium</i> sp 2	6						7				2		
<i>Stylidium</i> sp 3										3	5		
<i>Stylidium spathulatum</i> subsp <i>spathulata</i>	2		4				14		31	3	20		
<i>Stylidium spathulatum</i> subsp <i>acuminata</i>											5		
<i>Stylidium violaceum</i>	17		2										
Thymelaeaceae													
<i>Pimelea</i> sp (GWJ 4204)											2		
<i>Pimelea angustifolia</i>			4										
<i>Pimelea clavata</i>				10	14					1		4	
<i>Pimelea ferruginea</i>					3								
<i>Pimelea hispida</i>			13	30			14		23		5		
<i>Pimelea imbricata</i>								38	31				
<i>Pimelea longiflora</i>	69		32						15	3	2		
<i>Pimelea rosea</i>			6	40	66		14		8	1	8		
<i>Pimelea spectabilis</i>			2							24	28	8	
<i>Pimelea suaveolens</i> subsp <i>suaveolens</i>										1	8		
<i>Pimelea sylvestris</i>				20						11	11		
Tremandraceae													
<i>Platytheca galioides</i>											3		
<i>Tetratheca affinis</i>	2		4						23		38		
<i>Tetratheca filiformis</i>	2					27							
<i>Tetratheca hirsuta</i>	11					9				32	43	2	
<i>Tetratheca hispidissima</i>											2		
<i>Tetratheca setigera</i> ^p	9									6	8	3	
<i>Tremandra diffusa</i>	8									38	34	1	
<i>Tremandra stelligera</i>			4					13		73	8	72	
Violaceae													
<i>Hybanthus debilissimus</i>	2									20	28	2	
Xanthorrhoeaceae													
<i>Xanthorrhoea gracilis</i>	3		8							14	63		
<i>Xanthorrhoea preissii</i>	27	57	75	30	41	27	36	25	77	8	40		
Xyridaceae													
<i>Xyris flexifolia</i>						18							
<i>Xyris lanata</i>	2		6			36							
Zamiaceae													
<i>Macrozamia riedlei</i>	13		25						38	8	61	42	16

^a weed species;^a some specimens subsequently confirmed as *Schoenus caespitosus*;^b specimens at quadrat 1009 subsequently confirmed as *Schoenus multiglumis*;^c specimens at quadrat 4236 subsequently confirmed as *Schoenus trachycarpus*;^d some specimens subsequently confirmed as *Gahnia* sp Yelverton (G. J. Keighery 10820) and others as *Gahnia* sp aff *insignis*;^e some specimens subsequently confirmed as *Schoenus subflavus*;^f some specimens subsequently confirmed as *Schoenus submicrostachyus*;^g specimens at quadrat 1041 subsequently confirmed as *Mesemelaena graciliceps*;^h members of this species group amalgamated in analysis;ⁱ some specimens subsequently confirmed as *Restio crascens*;^j some amalgamation of this taxon in analysis including *Desmodiadus flexuosus* ms, *Empodisma gracillimum*, *Taraxis glaucescens* ms;^k some specimens subsequently confirmed as *Lepyrodia extensa*;^l some specimens subsequently confirmed as *Lepyrodia mura*;^m some specimens subsequently confirmed as *Chaetanthes leptocarpoides*;ⁿ subsequently confirmed as *Stylidium spathulatum*;^p some specimens subsequently confirmed as *Tetralthea hispidissima*.

Terrestrial invertebrates in south-west Australian forests: the role of relict species and habitats in reserve design

Barbara York Main

Department of Zoology, University of Western Australia, Nedlands WA 6907

Abstract

Invertebrates are an integral and functional component of any ecosystem, including the south-west Australian forests. However they are often overlooked in biological studies. This is partly due to the incompleteness of taxonomic knowledge, as much of the invertebrate fauna is unnamed. Also, while a great deal of distributional data exists for invertebrates, it is generally not readily accessible, often associated only with individually stored museum specimens and/or scattered taxonomic descriptions in the literature. It is proposed here that a pragmatic approach to invertebrate conservation via reservation is to consider the known distribution of selected relict species (because of their sensitivity to disturbance) and their microhabitat requirements, and (a) deduce whether such species/habitats are adequately included in the current reserve system and (b) if not, then predict where in the overall domain they are likely to occur, with a view to ensuring their persistence. A short-cut method is to note the location of Gondwanan-type sites and argue for their preservation on the grounds that they will contain relict species assemblages. This approach assumes that widespread and/or ecologically tolerant species are more likely to have other options in the face of artificial disturbance.

Introduction

In the catch-phrases of an attention-seeking society, while "big may be beautiful" in reference to the role of invertebrates in biological processes and ecosystems, perhaps the apt phrase is "small and significant". Wilson (1987) convincingly argued for the dependance on invertebrates of higher life forms, and the support base provided by invertebrates in any ecosystem. The decline of some local insectivorous birds is commonly remarked upon. Hence it is ironic that although nature conservation is now a well established and even "popular" discipline with a practical and ethical base, little attention has been given to invertebrates (in their own right) until relatively recently. In Australia, compared to vertebrates and flora, invertebrates have fared poorly with respect to conservation. Amongst the general publications devoted to invertebrates, those of New (1984, 1995) are notable, and there are also studies dealing with particular groups, for example a recent review on arachnid conservation by Yen (1995).

Under the blanket concept and ethos of conservation must be considered the practical manifestation: reservation of places for invertebrates. How then, if at all, does the practicality of reservation for terrestrial invertebrates differ from that for flora or vertebrates? Or can they be assumed to be safe-guarded along with whatever methods are applied in reserve establishment and management for the more obvious biota such as vascular plants and vertebrates? It must be noted that in spite of their significance, invertebrates are frequently overlooked in

broad sweep ecological studies and biological surveys because of their small size and often cryptozoic behaviour.

Nevertheless there are statutory requirements in Western Australia concerning the conservation of all fauna and dissemination of knowledge related to that fauna. The Strategic Plan 1995 of the Department of Conservation and Land Management (Anon 1995a) states under the major functions of CALM firstly, "*Conservation of Nature. To conserve the indigenous biota and ecological processes in natural habitats throughout the State*" and fourthly "*Knowledge. To ensure that functions [i.e. concerning conservation] are underpinned by up-to-date and reliable science-based knowledge.*" These objectives surely partner in intent the Western Australian Museum Act which charges the Western Australian Museum "*to make and preserve ... collections representative of the natural history of the State*" (Anon 1969). Furthermore the Science and Information Division of CALM has been developed to meet several inclusive needs; "*to document the biota, ecological processes & biological resources of the state*", "*to conserve threatened species & ecological communities by ameliorating inimical processes*", and "*to ensure that land & biological resources are used sustainably*" (Anon 1995a). This would suggest that all is well for our natural heritage (including the significant smaller "taxa") and that a beneficent authority is taking good care of our fauna and is about to inform us (if not already having done so) of what we have and will continue to have, within our south-west forests.

Invertebrates - a special case

However I argue here that if conservation reserves within the region under discussion within the 800mm rainfall isohyet (for instance forested landscapes) are to adequately cater for conservation of invertebrates then

the special characteristics and needs of this fauna must be considered. These needs stem primarily from one or more of the following characteristics and phenomena;

- the sheer diversity and taxonomic range of invertebrates. Some idea of this diversity can be gauged from spiders: this arachnid order is represented by at least 50 families in Western Australia of which all but a few occur in the south-west forest and some of which occur only in the region (Main 1985 and unpublished);
- the range of foraging methods from vegetative to predatory and parasitic;
- the range of life histories and individual longevity ranging from a few days to over 30 years;
- the differing dispersal methods, particularly of juveniles, and mobility of various life history stages;
- the range of site fidelity from sedentary to partially territorial or transitory;
- the interaction of life cycle patterns with other biota;
- the association with particular physiographic configurations; and
- the antiquity of many forms/taxa.

All the above phenomena/characteristics are a consequence of the historical ecology of the particular taxon especially of the "ancient" groups which has been determined by the environmental history of the landscape including geological and climatic changes and changes in the vegetation which relate to earlier continental configurations and their positions.

Because of their small size and often specialised behaviour, particularly of relict forms, many invertebrates (in contrast to most vertebrates) are confined to topographically or geographically restricted areas and specialised microhabitats which may not be readily perceived by broader scale surveys. Such microhabitats are vulnerable to artificial disturbances imposed by agriculture, forestry and other rural and urban disruptions to the landscape, for instance roads and other human constructions.

Current knowledge-base of invertebrates

We might digress now and look at our current knowledge-base relating to invertebrates of the south-west forest of Western Australia by asking the following question. Is there a taxonomic database (either as lists of taxa contained in the Western Australian Museum and/or other collections or in the published literature), arranged or accessible according to the region in the present context, habitat data, and whether present in the current reserve system?

Firstly there is a great deal of information on local distributions of invertebrate taxa for the south-west forest region in the taxonomic literature. Nearly 3000 papers dealing with all aspects of invertebrates of Western Australia are listed in the excellent bibliography compiled over 15 years ago by Majer & Chia (1980). In spite of this, the taxonomic and distributional data needed now are not readily or rapidly accessible and are

largely uncoordinated, except for particular groups which specialists have in their personal research files. For example a recent paper by Abbott (1994) discusses the distribution of earthworms in the south-west and shows a spatter of dots on a map within the 400mm rainfall zone. The data were derived from museum collections and published records but are not readily accessible. Similarly, many systematists including myself (for spiders) have unpublished species lists from particular parks or localities.

Secondly, some associated habitat data accompany stored specimens and taxonomic literature records, but except for a very few groups are either uncoordinated or unpublished.

Thirdly, the greater proportion of the invertebrate fauna (and not just insects) is unnamed. Hence biological and distribution data associated with stored specimens, as well as being not readily accessible, cannot be manipulated in the same way as vertebrate data. Statements such as, "All states and the Commonwealth have a database of threatened and rare species observations", from the Deferred Forests Assessment document (DFA, Anon 1995b, p 5) are largely irrelevant for invertebrates as such databases refer almost exclusively to vertebrates. However, Abbott (1995) has produced a valuable resource in his selective list of insects recorded in the literature from the jarrah and karri forests of southwestern Western Australia; he noted "nearly 1800 insect and closely allied species of ... Hexapoda" from south-west forests but estimated that the total number could be 15 000 to 20 000.

Suggested guide-lines for reservations

In spite of the absence of comprehensive, usable databases of invertebrates, a case study could be made of selected taxa to determine guidelines for reserve selection. This could be based on what knowledge we do have regarding relictual taxa including Gondwanan elements (e.g. spiders and other arachnids, selected insects, amphipods, earthworms, nemertean, Onychophora etc), which are confined to certain habitats and in some cases geographic areas. Bearing in mind the foregoing points regarding the restricted nature and vulnerability of habitats of relic taxa, the converse is assumed for later evolved/adapted groups and/or more widespread taxa, when such taxa are likely to be more resilient to artificial disturbance and fragmentation of habitats.

Definition of relict taxa and habitats

Some definition of relict taxa and their associated habitats needs to be made. Generally such taxa are representative of a fauna from a more humid, less markedly-seasonal climate associated with a mesophytic forest with closed canopy and as such they are relicts of a pre-fire-prone environment. With progressively dryer and more seasonal climatic conditions, the most favourable habitats have become increasingly fragmented until now such fauna are restricted to specialised *microhabitats* which simulate on a small scale an earlier more widespread habitat. Relict taxa include extremely ancient representatives of Gondwanan

elements and with lineages reaching back to pre-Cretaceous times (120 - 140 million years ago) e.g. the trapdoor spider *Moggridgea* (see Main 1991) and velvet worms (*Onychophora*) or to the early Tertiary Eocene/Oligocene period 40 - 50 mya (Main 1987). Striking austral zoogeographic affinities are found within many spider families, including the Archaeidae and Pararchaeidae (Forster & Platnick 1984; Platnick 1991; Main 1995), Orsolobidae (Forster & Platnick 1985; Griswold & Platnick 1987), which can best be interpreted as relict distributions from a contracted early Tertiary environment. Presence of the Micropholcommatidae and Archaeidae in south-western Western Australia has been explained in this manner (Main 1974, 1995). The distribution of certain terrestrial insect groups such as thrips of the family Aeolothripidae (Mound 1972) can also be interpreted to be of this era.

Many groups of invertebrates from both periods have taxonomic affinities with south-eastern Australia, Tasmania, New Zealand and/or other southern continents. It is outside the scope of this paper to document the many examples which, from perusal of the taxonomic literature indicate Gondwanan affinities. Some relationships are listed by Main & Main (1991) and Hopper *et al.* (1996).

The associated habitats of relict species are permanently moist and shaded, with such conditions provided by high rainfall. However other formative physiographic conditions include topography, proximity to coast and directional orientation. Main & Main (1991), Hopper *et al.* (1996), and A R Main (1996) have summarised the major characteristics of persistent Gondwanan habitats in south-west Western Australia. In addition B Y Main (1996) has demonstrated the occurrence of relictual Gondwanan microhabitats on the plateau region of southern Western Australia.

Location of relict habitat sites

The major high rainfall areas on geologically old terrain include the Walpole/Nornalup topographically high region, the high etched region west of Manjimup and Pemberton and farther north, and isolated regions near Collie, Dwellingup and Jarrahdale. Areas which are wet by virtue of old erosional phenomena combined with orientation include the northern valleys of the Darling Scarp such as near Mundaring and Kalamunda, and farther south in the sinuous configurations of rivers, such as the Deep River, which have further significance by having a continuity with the fauna of the Walpole/Nornalup area. Noteworthy also are some Pleistocene sites (including cave complexes) and areas of the Perth Coastal Plain, as at Jandakot, where relict fauna has encroached from "older" areas. Farther south the limestones of the Mammoth Cave area and Boranup with high rainfall and wet karri forest contain certain relicts.

Typical minor or "special" areas are sites associated with granite outcrops which benefit from run-off (sometimes created simply by dew and light mist), summits of emergent monadnocks and south facing slopes, swampy headwaters of river systems, perched "swamps" and so on. Even within the general forest, regardless of minor topography, there are further secretive "micro-sites"

such as; the litter "stacks" or "rings" around the butts of karri and accumulated debris in the buttresses of tingle (Wallis 1992); the persistent spongy (if not recently burnt) bark of red tingle; long unburnt rotten logs; stag-heads of old trees and debris in tree forks (particularly sheoaks) and trunk crevices.

As well as high rainfall, the prevalence of fog whether induced by topography or coastal proximity, promotes persistence of wet "microhabitats". Examples are remnants of the old plateau (including Mt Cooke and Mt Saddleback in the jarrah forest), Mt Lindesay near Denmark, granite outcrops and south coast peninsulas such as Torndirrup and West Cape Howe. Again, within such sites subtle microhabitats can be further specified.

From the foregoing it is apparent that when considering reservations of sites to include invertebrates (whether at the species or community level), different, smaller scale criteria need to be used than is the case for vertebrates.

The DFA document (Anon 1995b) emphasises the importance of using physical environmental data in the absence of adequate community data "to ensure that representativeness is met". This approach is paramount in the selection of reserves encompassing invertebrate preservation.

Bench-mark information

Contained within the stored collections and literature records is extractable bench-mark information of distributions of taxa prior to continuing disturbance. Notable are the reports of the Michaelsen & Hartmeyer Expedition to south-western Western Australia in 1905 (Michaelsen & Hartmeyer 1907-30). Nearly 90 sites were sampled, of which about 25 were in the forest-zone extending from Jarrahdale to Nornalup and Albany. Within the forest and neighbouring areas, accessibility was both facilitated and constrained by forestry activities ranging from logging and milling to timber transport and loading of ships at Bunbury, Hamelin Bay and Torbay. Ironically it is the contemporary timber industry that is provoking most research and fortuitous gathering of collections and knowledge of much of the invertebrate fauna of the forest.

Collection methods in 1905 were both haphazard and less refined than some of the current techniques and the collectors did not have our hindsight of environmental and taxonomic knowledge to be able to predict where relict (Gondwanan) species would be likely to occur. Nevertheless it is notable that this expedition was staged on the premise that the south-west peninsula of Australia would be the biogeographic complement of the southern areas of South America and South Africa which regions the German team had already sampled. Later taxonomic studies confirm this premise.

The relevance of the bench-mark collections, in combination with later records, to the selection of reserves must not be ignored.

Summary

I suggest that by selecting named relict taxa, noting their microhabitat requirements, predicting where such

microhabitats are likely to occur in the forest, and combining the above with recorded locality data for such relict taxa, then it should be possible to deduce whether all known relict taxa and their full geographic ranges are represented within the present reserve system, and conversely whether all "relict" sites and concomitant, potential unnamed species are catered for in the present reserve system.

Obviously we don't have the luxury of time to ferret out even the recorded information of species, habitats and distributions to impose these data as a template on the geographic area. However, this needs to be done, taxon by taxon by various specialists in a co-ordinated manner.

The practical short-cut suggested here places priority on physiographic features likely to contain any of the microhabitat categories described above and as delineated by Main & Main (1991), A R Main (1996), B Y Main (1996) and Hopper *et al.* (1996), and indeed where our major biotrove lies. I suggest that this approach is an ideal guide for selection of reserves containing microhabitats appropriate to relict, geographically restricted and specialised invertebrates. The more widespread and/or ecologically tolerant species have a wider range of natural options and are also better able to cope with artificially disrupted habitats.

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Aquatic fauna of the Warren bioregion, south-west Western Australia: Does reservation guarantee preservation?

K M Trayler¹, J A Davis¹, P Horwitz² & D Morgan¹

¹School of Biological and Environmental Sciences, Murdoch University, Murdoch WA 6150;

²Centre for Ecosystem Management, Edith Cowan University, Joondalup WA 6027

Abstract

The Warren Bioregion, in the extreme south-west of Western Australia, has a unique assemblage of aquatic invertebrates, fish and amphibians. Current literature indicates that 192 fully described species have been collected, of which 10 invertebrate, 1 fish and 6 frog species could be considered locally endemic. We estimate that secure nature reserves (A-Class and National Parks) in the Warren Bioregion provide a refuge for 86% of the aquatic faunal elements. Reservation alone, however, may not be sufficient to protect certain of the aquatic fauna. Adverse impacts occurring within catchments, including erosion and deposition of sediment, salinization, fire, land clearing, the presence of dams and the introduction of exotic fish, may adversely affect the aquatic fauna within a reserve. Management of protected habitats must ensure that only anthropogenic activities which are sympathetic to the long term persistence of all elements of the biota occur within, and adjacent to, the reserve systems.

Introduction

The natural landscape of the south-western corner of Australia is characterised by rivers which arise on an ancient and flat semi-arid inland plateau. From here, the rivers flow sluggishly towards the coast, before passing through a zone where the topography steepens and rainfall increases (Mulcahy *et al.* 1972; Churchward *et al.* 1988). Beyond this, the rivers again slow as they traverse the coastal lowlands, which feature extensive wetland systems and terminate in lagoon-like estuaries. Early settlers found the coastal lowlands to be largely infertile soils and used much of the area as pastoral land, preferring to use the rich alluvial soils along the rivers for intensive agriculture (Jarvis 1979). Pressures of urbanization and intensification of agriculture, associated with a burgeoning population in the century since colonization, have led to the loss of a large proportion of coastal wetland systems and many of those that remain have been altered from their natural state (see Halse 1989). A number of the larger rivers have been damaged through siltation and salinization, and many of the remainder are now impounded or subject to varied degrees of alteration through activities such as mining and logging (Olsen & Skitmore 1991).

The effect of these changes on the aquatic fauna cannot be fully assessed due to the lack of historical or baseline data. Locally or even regionally endemic aquatic species may have been lost from south-western Australia, or suffered substantial range reductions, particularly where these fauna were sensitive to changed hydrological regimes, increased eutrophication and/or salinization. This is evident in our aquatic environments today. Highly eutrophic wetlands contain few rare taxa,

have high densities of "pollution tolerant" species and, overall, support an invertebrate composition which is distinct from that occurring in low to moderately enriched or coloured wetlands (Davis *et al.* 1993; Edward *et al.* 1994). The highly saline Hotham River and Thirty-Four Mile Brook, south-east of Perth, are dominated by salt tolerant crustaceans (60% total abundance), while insects contribute only 14% to the overall invertebrate composition (Bunn & Davies 1992). This situation is atypical of undisturbed streams of the jarrah forest, where insects usually comprise 70-80% of the fauna (Bunn *et al.* 1986), and was attributed to increased salinity (Bunn & Davies 1992). Williams *et al.* (1991) found little or no longitudinality in the faunal composition of the Blackwood River despite the presence of a distinct salinity gradient along its length. Although this could be interpreted as evidence of a halotolerant fauna, it may also indicate elimination of less tolerant fauna, which once characterised a more diverse system.

Public awareness of the need to conserve aquatic habitats has increased markedly over the last decade and this is reflected in the number of scientific studies that have been undertaken on wetlands, streams and rivers in the south-west since the mid 1980s (see Balla 1994). Considerable attention has been devoted to the aquatic fauna and their habitats in highly populated areas of the south-west, such as wetlands on the Swan Coastal Plain and streams in the adjacent jarrah forest, where monitoring to assess the impact of pollution or habitat change has often been the principal research or management objective (*e.g.* Storey *et al.* 1990; Bunn & Davies 1992; Grouns *et al.* 1992).

Further south, the relatively undisturbed aquatic habitats within the Warren Bioregion (*sensu* Thackway & Cresswell 1995) have also provided a focus for scientific studies (*e.g.* Christensen 1982; Pusey & Edward 1990a, b; Horwitz 1996; Edward *et al.* 1994). This region is regarded as an important centre for endemism from a

botanical viewpoint (Hopper *et al.* 1992), but its significance to the aquatic fauna has not been assessed in its entirety. This paper summarizes existing knowledge of the aquatic fauna in the Warren Bioregion and estimates the degree of endemism found in the region. In addition, it presents a preliminary assessment of the reservation status of known aquatic species and makes recommendations for the ongoing protection of fauna within the reserve system.

Approaches

The aquatic invertebrates (>110 µm), fishes and amphibians which occur within the Warren Bioregion were compiled from published literature and museum records, and are therefore limited by the habitats examined and sampling protocol of these sources. The distribution of each species, determined from published literature, is described as either widespread, regionally endemic or locally endemic in accordance with Horwitz (1996). The reservation status of each species within the Warren Bioregion has been determined according to their presence or absence within reserves which fall under categories I and II of the World Conservation Union's classification of protected areas (Anon. 1994). This equates only to nature reserves (A-Class) and national parks which have the conservation of flora and fauna as a primary objective and require legislative provisions to alter their boundaries or status. Other forms of reserves in the region do not have this level of security and therefore have not been included in this study. We do, however, acknowledge that these other areas also play an important role in conservation. For the purpose of this study, a species which is described as reserved must have been recorded at least once in a secure reserve, as defined above.

To date, there have been no comprehensive surveys of aquatic invertebrates within all nature reserves and national parks of the Warren Bioregion and therefore the reference in Table 1 to species as absent from these reserve categories should be considered preliminary. In addition, species which are widespread or regionally endemic may not be found in nature reserves or national parks within this region, but may be found within similar reserves located elsewhere.

Although more invertebrate taxa are found in the Warren Bioregion than have been recorded in Table 1, many of these have not yet been described and specimens only exist in voucher or reference collections of individual researchers. To prevent confusion, whereby authors may have assigned different voucher names to the same taxon, only species for which published descriptions exist were considered here. Emergent adult invertebrates found in the vicinity of aquatic habitats were excluded because they could not be definitively linked with specific waterbodies. In addition, waterbirds have been excluded from this review, but information relating to their occurrence and reservation within the larger southern forest region may be found in Christensen (1992).

The tabulated information on aquatic invertebrates, fishes and amphibians provides a preliminary account of the level of endemism of aquatic fauna in the Warren

Bioregion and emphasises the importance of the reserve system to both the restricted and more common fauna of the region.

Local endemism in the aquatic fauna of the Warren Bioregion

Invertebrates

Aquatic habitats within the Warren Bioregion support a large proportion of invertebrate taxa which are endemic to south-west Western Australia, with approximately 17% of these considered locally restricted on the basis of surveys (Table 1). This number, however, may be an underestimate as only fully-described species have been considered, thereby excluding some taxa. There are, for example, only eight oligochaete species with widespread distributions shown in Table 1, yet there are at least a further four species which are restricted to the Warren Bioregion (Horwitz 1996) for which descriptions are pending (A Pinder *pers. comm.*). This situation may also extend to other groups, notably the dipterans and arachnids. Locally endemic invertebrates include the freshwater crayfish *Engaewa subcoerulea* and *E. similis* and the trichopteran *Kosrheithrus boorarius* (see Horwitz 1994; Grouns & Davis 1994, respectively).

A rich suite of micro-crustaceans have been found in the area and, in the case of the copepods, this is highly distinctive (Table 1). Bayly (1992) examined temporary ponds near Northcliffe and identified several copepods which are locally endemic, including *Calamoecia elongata*, *Boeckella geniculata* and *Paracyclops* sp. nov., as well as a unique form of *C. tasmanica* sl. In addition, the copepod *Hemiboeckella powellensis* is known only from Lake Powell, between Albany and Denmark (Bayly, 1979). Locally endemic cladocerans, *Biaptera imitaria* and *Daphnia occidentalis* were also found near Northcliffe by Bayly (1992). *Daphnia occidentalis* is a relictual species thought to have originated 70 mybp (Benzie 1986, 1988). This species was found in large numbers in a single pool, surrounded by swamp land within the D'Entrecasteaux National Park.

Fish

Eight species of freshwater fish are endemic to the south-west of Western Australia (Table 2) and four of these are now principally confined to the Warren Bioregion (Morgan *et al.* 1996). These include the Western Australian salamanderfish *Lepidogalaxias salamandroides*, a relictual Gondwanaland species (Allen 1982), which is now predominantly restricted to ephemeral pools within the coastal peat flats between Windy Harbour and Walpole (Morgan *et al.* 1996). The black stripe minnow *Galaxiella nigrostriata* and Balston's pygmy perch *Nannatherina balstoni* are similarly confined, although the former species is found in low numbers in a few lakes of the region, while the latter occurs in low numbers in both lakes and rivers of the region (Morgan *et al.* 1996). The mud minnow *Galaxiella munda* has the widest distribution of these four species, occurring in the headwaters and tributaries of rivers, as well as on the coastal peat flats (Morgan *et al.* 1996).

Disjunct and isolated populations of some of these

Table 1

Invertebrate fauna found in aquatic habitats within the Warren bioregion. Reservation status refers to their presence or absence in a nature reserve or national park within the bioregion. Distribution: W, widespread; RE, regionally endemic; LE, locally endemic. Sources: 1, Pusey & Edward (1990a); 2, Grouns & Davis (1994); 3, Edward *et al.* (1994); 4, Bayly (1982); 5, Horwitz (1994); 6, Williams *et al.* (1991); 7, Bayly (1992); 8, Bayly (1979); 9 Harvey (1996); 10, Morton (1990).

Species ¹	Source	Lotic	Lentic	Reservation	Distribution
MOLLUSCA					
Hydriidae					
<i>Westralunio carteri</i> Iredale	2,3	√	√	+	RE
Glacidorbidae					
<i>Glacidorbis occidentalis</i> Bunn & Stoddart	1	√		+	RE
Ancylidae					
<i>Ferrissia petterdi</i> Johnston	1		√	+	W
Hydrobiidae					
<i>Potamopyrgus niger</i> Quoy & Gaimard	6		√	–	W
ANNELIDA					
Phreodrilidae					
<i>Insulodrilus lacustris</i> Benham	5		√	+	W
<i>Insulodrilus nudus</i> Brinkhurst & Fulton	5		√	+	W
Tubificidae					
<i>Limnodrilus hoffmeisteri</i> Cleperede	5		√	+	W
Naididae					
<i>Pristina longiseta</i> Ehrenberg	5		√	+	W
<i>Pristina aquiseta</i> Bourne	5		√	–	W
<i>Dero furcatus</i> Muller	5		√	–	W
<i>Dero digitata</i> Muller	5		√	+	W
<i>Chaetogaster diastrophus</i> Gruithuisen	5		√	–	W
ARACHNIDA					
Hydryphantidae					
<i>Pseudohydryphantes doegi</i> Harvey	5		√	+	RE
Aturidae					
<i>Wheenyoides cooki</i> Harvey	5		√	+	RE
Limnochareidae					
<i>Limnochares australica</i> Lundblad	5		√	+	W
Pionidae					
<i>Australotiphys barmutai</i> Harvey	9		√	+	RE
<i>Larri laffu</i> Harvey	9		√	+	RE
<i>Piona cumberlaudensis</i> Rainbow	9		√	+	W
Arrenuridae					
<i>Arrenurus</i> sp nr <i>tasmanicus</i> Lundblad	5		√	+	RE
OSTRACODA					
Limnocytheridae					
<i>Limnocythere mowbrayensis</i> Chapman	1,3	√	√	+	W
<i>Gomphiodella aff maia</i> De Deckker	3		√	+	W
Cyprididae					
<i>Candonocypris novaezelandiae</i> Baird	2,3	√	√	+	W
<i>Newnhamia fenestra</i> King	3		√	+	W
<i>Cypretta viridis</i> Thomson	7		√	+	W
<i>Cypretta baylyi</i> McKenzie	3,4,7		√	+	W
<i>Eucypris virens</i> Jurine	7		√	+	W
<i>Kapcypridopsis asymmetra</i> De Deckker	4		√	+	LE
<i>Sarcypridopsis aculeata</i> Costa	3		√	+	W
<i>Alboa wooroa</i> De Deckker	3		√	+	W
<i>Ilyodromus candonites</i> De Decker	4		√	+	LE
<i>Ilyodromus varrovillus</i> King	7		√	+	W
<i>Bennelongia australis</i> Brady	8		√	+	W
Candonidae					
<i>Candonopsis tenuis</i> Brady	3		√	+	RE
COPEPODA					
Centropagidae					
<i>Calamoecia attenuata</i> Fairbridge	1,3,7	√	√	+	RE
<i>Calamoecia tasmanica</i> Smith sl	1,3,7	√	√	+	W
<i>Calamoecia elongata</i> Bayly	7		√	+	LE
<i>Hemiboeckella scarli</i> Sars	3,7		√	+	W
<i>Hemiboeckella andersonae</i> Bayly	3,7		√	+	RE
<i>Hemiboeckella powellensis</i> Bayly	8		√	+	LE
<i>Boeckella geniculata</i> Bayly	7		√	+	LE

Species	Source	Lotic	Lentic	Reservation	Distribution
<i>Gladioferens imparipes</i> Thomson	3		√	+	RE
Cyclopidae					
<i>Macrocylops albidus</i> Jurine	1,7	√	√	+	W
<i>Australocylops australis</i> Sars	7		√	—	W
<i>Eucyclops spatulatus</i> Morton	10		√	—	W
CLADOCERA					
Chydoridae					
<i>Biapertura cf macrocopa</i> Sars	4,7		√	+	W
<i>Biapertura rigidicaudis</i> Smirnov	4		√	+	W
<i>Biapertura affinis</i> Leydig	1	√	√	+	W
<i>Biapertura longinqua</i> Smirnov	7		√	+	W
<i>Biapertura nr setigera</i> Brehm	3		√	+	W
<i>Biapertura imitatoria</i> Smirnov	7		√	+	LE
<i>Graptoleberis testudinaria</i> Fischer	3		√	+	W
<i>Camptocercus cf australis</i> Sars	3		√	+	W
<i>Chydorus barroisi</i> Richard	4		√	+	W
<i>Chydorus cf sphaericus</i> O F Muller	7		√	—	W
<i>Pleuroxus inermis</i> Sars	7		√	—	W
<i>Pleuroxus jugosus</i> Henry	4		√	+	W
<i>Alonella cf excisa</i> Fischer	7		√	+	W
<i>Rak obustus</i> Smirnov & Timms	8		√	—	W
<i>Monope reticula</i> Henry	7		√	+	RE
Macrothricidae					
<i>Neothrix armata</i> Gurney	1,3,4,7	√	√	+	W
Daphniidae					
<i>Simoccephalus acutirostratus</i> King	1,3	√	√	+	W
<i>Daphnia carinata</i> King sl	3		√	+	W
<i>Daphnia occidentalis</i> Benzie	7		√	+	LE
<i>Scapholeberis kingi</i> Sars	7		√	+	W
Bosminidae					
<i>Bosmina meridionalis</i> Sars	3		√	+	W
ISOPODA					
Amphisopidae					
<i>Amphisopus annectans</i> Nicholls	1,5		√	+	RE
<i>Amphisopus ?lintoni</i> Nicholls	1	√	√	+	RE
<i>Hyperodesipus ?plumosus</i> Nicholls & Milner	2	√		—	RE
AMPHIPODA					
Perthidae					
<i>Perthia acutitelson</i> Straskraba	1,2	√	√	+	RE
<i>Perthia branchialis</i> Nicholls	3		√	—	RE
Ceinidae					
<i>Austrochiltonia subtenuis</i> Sayce	3		√	+	W
DECAPODA					
Parastacidae					
<i>Cherax quinquecarinatus</i> Gray	3,5		√	+	RE
<i>Cherax tenuimanus</i> Smith	3,5		√	+	RE
<i>Cherax preissii</i> Erichson	5		√	+	RE
<i>Cherax crassimanus</i> Riek	5		√	+	RE
<i>Cherax destructor</i> Clark	3		√	+	W
<i>Engaewa subcoerulea</i> Riek	5		√	+	LE
<i>Engaewa similis</i> Riek	5		√	+	LE
Grapsidae					
<i>Leptograpsodes octodentatus</i> Milne-Edwards	5		√	+	W
Palaemonidae					
" <i>Palaemonetes</i> " <i>australis</i> Dakin	3,5		√	+	RE
ANISOPTERA					
Aeshnidae					
<i>Aeshna brevistyla</i> Rambur	3		√	+	W
<i>Austroaeschna anacantha</i> Tillyard	2,5,6	√	√	+	RE
Corduliidae					
<i>Orthetrum caledonicum</i> Brauer	3,5,6	√	√	+	W
<i>Austrothemis nigrescens</i> Martin	3,5		√	+	W
<i>Diplacodes bipunctata</i> Brauer	5		√	—	W
<i>Nannophya dalei occidentalis</i> Tillyard	5		√	+	RE
<i>Lathrocordulia metallica</i> Tillyard	3		√	+	RE
<i>Hesperocordulia berthoudi</i> Tillyard	3		√	+	RE

Species	Source	Lotic	Lentic	Reservation	Distribution
<i>Hemicordulia australiae</i> Rambur	3,6	√	√	+	W
<i>Hemicordulia tau</i> Selys	5		√	+	W
<i>Procordulia affinis</i> Selys	3,5		√	+	RE
<i>Synthemis cyanitincta</i> Tillyard	2,3,5	√	√	+	RE
Gomphidae					
<i>Hemigomphus armiger</i> Tillyard	2	√		—	RE
<i>Austrogomphus lateralis</i> Selys	2,3	√	√	+	RE
<i>Austrogomphus collaris</i> Hagen	3,5		√	+	W
<i>Austrogomphus oclraceus</i> Selys	6	√		—	W
ZYGOPTERA					
Lestidae					
<i>Austrolestes annulosus</i> Selys	3,5		√	+	W
<i>Austrolestes analis</i> Rambur	5		√	+	W
Megapodagrionidae					
<i>Argiolestes minimus</i> Tillyard	5		√	+	RE
<i>Austroagrion cyane</i> Selys	3		√	+	W
<i>Xanthagrion erythroneurum</i> Selys	6	√		—	W
EPHEMEROPTERA					
Leptophlebiidae					
<i>Bibulmena kadjina</i> Dean	1,2,3	√	√	+	RE
<i>Neboissophlebia occidentalis</i> Dean	3		√	+	W
<i>Nyungara bunui</i> Dean	1,2	√		+	RE
<i>Nyungara ellitasha</i> Dean	2	√		—	W
Caenidae					
<i>Tasmanococuis tillyardi</i> Lestage	2,3	√	√	+	W
PLECOPTERA					
Gripopterygidae					
<i>Newmanoperla exigua</i> Kimmins	1,2	√	√	+	RE
<i>Leptoperla australica</i> Enderlain	1,2	√		+	RE
MEGALOPTERA					
Corydalidae					
<i>Archichauliodes cervulus</i> Theischinger	2	√		—	W
TRICHOPTERA					
Leptoceridae					
<i>Lectrides parilis</i> Neboiss	1,2	√	√	+	RE
<i>Triplectides australis</i> Navas	3		√	+	W
<i>Condocerus nr aptus</i> Neboiss	2	√		—	RE
<i>Notoperata tenax</i> Neboiss	3		√	+	RE
Atriplectididae					
<i>Atriplectides dubius</i> Mosely	2,3	√	√	+	W
Hydroptilidae					
<i>Acroptila globosa</i> Wells	1,3		√	+	RE
Ecnomidae					
<i>Ecnomiina ?trulla</i> Neboiss	1,3	√	√	+	RE
<i>Ecnomus pansus</i> Neboiss	1,3		√	+	W
<i>Ecnomus turgidus</i> Neboiss	3		√	—	W
Philorheithridae					
<i>Kosrheithirus boorarus</i> Neboiss	2	√		—	LE
Hydrobiosidae					
<i>Apsilochorema urdalum</i> Neboiss	2	√		—	RE
<i>Taschorema pallescens</i> Banks	2	√		—	RE
Hydropsychidae					
<i>Smicrophylax australis</i> Ulmer	2	√		—	RE
Polycentropodidae					
<i>Plectrocnemia eximia</i> Neboiss	3		√	+	W
<i>Adectophylax volutus</i> Neboiss	2	√		—	RE
COLEOPTERA					
Dytiscidae					
<i>Sternopriscus ?browni</i> Sharp	1,3	√	√	+	RE
<i>Sternopriscus marginatus</i> Watt	1	√		+	RE
<i>Homoeodytes scutellaris</i> Germar	1,3		√	+	W
<i>Rhantus suturalis</i> MacLeay	1	√	√	+	W
<i>Liodessus inornatus</i> Sharp	3		√	+	RE
<i>Liodessus dispar</i> Sharp	3		√	+	RE

Species	Source	Lotic	Lentic	Reservation	Distribution
<i>Megaporus solidus</i> Sharp	3		√	+	RE
<i>Necterosoma dartwini</i> Babington	3		√	+	RE
<i>Antiporus femoralis</i> Boheman	3		√	+	W
<i>Lancetes lanceolatus</i> Clark	3		√	+	W
DIPTERA					
Simuliidae					
<i>Austrosimulium furiosum</i> Skuse	1,5	√	√	+	W
<i>Cnephia tonnoiri tonnoiri</i> Drummond	5		√	-	W
Chironomidae					
<i>Aphroteniella filicornis</i> Brundin	1,2,3,5	√	√	+	W
<i>Aphroteniella tenuicornis</i> Brundin	5		√	-	W
<i>Paramerina levidensis</i> Skuse	1,2,3,5	√	√	+	W
<i>Procladius palludicola</i> Skuse	3,5		√	+	W
<i>Procladius ?villosimanus</i> Kieffer	3		√	+	W
<i>Alotanypus dalyupensis</i> Freeman	1,3,5		√	+	W
<i>Coelopynia pruinosa</i> Freeman	3		√	+	W
<i>Corynoneura ?scutellata</i> Winnertz	5		√	+	W
<i>Stictocladius uniserialis</i> Freeman	1,5	√	√	+	W
<i>Cricotopus annuliventris</i> Skuse	1,2,3,5	√	√	+	W
<i>Paralimnophyes pullulus</i> Skuse	3,5		√	+	W
<i>Cladopelma curtivalva</i> Kieffer	1,3,5	√	√	+	W
<i>Cryptochironomus griseidorsum</i> Kieffer	1,3,5	√	√	+	W
<i>Chironomus occidentalis</i> Skuse	3		√	+	W
<i>Chironomus aff alternans</i> Walker	1,3,5		√	+	W
<i>Chironomus tepperi</i> Skuse	4		√	+	W
<i>Dicrotendipes ?conjunctus</i> Walker	1,3,5	√	√	+	W
<i>Kiefferulus martini</i> Freeman	1,3,5	√	√	+	W
<i>Kiefferulus intertinctus</i> Skuse	3,5		√	+	W
<i>Paratanytarsus grimmii</i> Schneider	5		√	+	W
<i>Stempellina ?australiensis</i> Freeman	3,5		√	+	W

¹ fully described species only

Table 2

Native fish species found in freshwater habitats in the Warren Bioregion. Reservation refers to their presence or absence within a nature reserve (A-class) or national park within the region. Distribution: W, widespread; RE, regionally endemic; LE, locally endemic. Sources of information include Christensen (1982), Jaensch (1992), Morgan *et al.* (1996) and Western Australian Museum records.

Species	Lotic	Lentic	Reservation	Distribution
AGNATHA				
Geotriidae				
<i>Geotria australis</i> Gray	√		+	W
TELEOSTEI				
Lepidogalaxiidae				
<i>Lepidogalaxias salmandroides</i> Mees		√	+	LE
Galaxiidae				
<i>Galaxiella nigrostriata</i> Shipway		√	+	RE
<i>Galaxiella munda</i> McDowall	√	√	+	RE
<i>Galaxias occidentalis</i> Ogilby	√	√	+	RE
<i>Galaxias truttaceus</i> Cuvier	√	√	+	W
<i>Galaxias maculatus</i> Jeys	√	√	+	W
Percichthyidae				
<i>Bostockia porosa</i> Castelnau	√	√	+	RE
Nannoperccidae				
<i>Edelia vittata</i> Castelnau	√	√	+	RE
<i>Nannatherina balstoni</i> Regan	√	√	+	RE
Plotosidae				
<i>Tandanus bostocki</i> Whitley	√	√	+	RE
Gobiidae				
<i>Pseudogobius olorum</i> Sauvage	√	√	+	W ¹
<i>Afurcagobius suppositus</i> Sauvage	√	√	+	RE ¹
Atheriniidae				
<i>Leptatherina wallacei</i> Prince, Ivantsoff & Potter	√	√	+	RE ¹

¹ not strictly a freshwater species.

species have been recorded from Margaret River, Bunbury, Gingin and Two Peoples Bay (Museum Records; Morgan *et al.* 1996) suggesting that they were once more widely distributed throughout the coastal environment of south-west Western Australia. All of these fishes are either included or have been recommended for inclusion in the list of Australian threatened fishes (Anon. 1994).

Amphibians

Twenty two species of frogs are found in the Warren Bioregion, with three of these occurring just within its boundaries (Table 3). Six of the remaining eighteen species could be considered to be locally endemic, including the south coast froglet *Ranidella subinsignifera*, the roseate frog *Geocrinia rosea*, the Walpole frog *G. lutea*, the white-bellied frog *G. alba*, the orange-bellied frog *G.*

vitellina and the sunset frog (Myobatrachidae). All four *Geocrinia* species and the sunset frog have highly limited geographic distributions with *G. vitellina* and *G. alba* formally gazetted in the schedules of the Commonwealth's Endangered Species Protection Act, 1992.

The Reserve System

The Warren Bioregion extends over 1 042 000 ha with approximately 25% of that area held as national parks or nature reserves (A-class). We estimate that these reserves incorporate 86% of the aquatic faunal elements found in the region, but 7% of locally restricted species are apparently not included (Table 4). The further inclusion of locally endemic species or assemblages into the reserve system is made difficult because they are often rare as well as restricted in their distribution. Large-scale surveys across all aquatic habitats within the lower south-west would be necessary to locate all of these aquatic fauna. This is unlikely to occur in the near future and so the ability to predict the occurrence of these fauna at unsurveyed sites would be advantageous.

Predictable patterns of faunal communities often occur in wetlands with similar physical and chemical characteristics (e.g. Edward *et al.* 1994). Thus, it may be possible to give priority for reservation to aquatic habitats with particular biophysical traits which, elsewhere, support high levels of endemic species. Highly acidic environments and aquatic habitats associated with granite outcrops provide good examples. The four species of copepod, and two species of cladoceran found by Bayly (1992) were all acidophilic and were collected from ponds with low pH. Two species of ostracod, *Ilyodromus candonites* and *Kapcypridopsis asymmetra*, and one species of chironomid, *Allotrissocladius* sp, which are endemic to the Warren Bioregion, have been found in temporary pools associated with granite outcrops (Bayly 1982). In addition, the sunset frog, which is thought to have originated approximately 30-36 million years ago was recently found in an organic-rich swamp at the base of a granite outcrop near Walpole (Roberts *et al.* 1997).

Granite outcrops and other areas elevated above the level of the Eocene marine incursion, such as headwater regions, permanent freshwater flows, and elevated coastal locations receiving orographic rainfall, often support relictual fauna (Main & Main 1991; Hopper *et al.* 1996). These relictual habitats generally provide organically rich and permanently moist microhabitats (Main & Main 1991) for a fauna which has persisted since eustatic changes and the onset of seasonal aridity in the early Tertiary (Keast 1981). Relictual fauna are of exceptional importance from a nature conservation perspective and thus the systematic evaluation of existing reserves and

Table 3

Frog species known to occur within the boundaries of the Warren Bioregion. Reservation refers to their presence or absence in a nature reserve (A-class) or national park within the region. Distribution: RE, regionally endemic; LE, locally endemic. Sources of information include Main (1965), Christensen (1992), Tyler *et al.* (1994), Roberts *et al.* (in press) and Wardell-Johnson (*pers. comm.*).

Species	Reservation	Distribution
Hylidae		
<i>Litoria adelaidensis</i> Gray	+	RE
<i>Litoria moorei</i> Copeland	+	RE
Myobatrachidae		
<i>Limnodynastes dorsalis</i> Gray	+	RE
<i>Heleioporus mornatus</i> Lee & Main	+	RE
<i>Heleioporus eyrei</i> Gray	+	RE
<i>Heleioporus psammophilus</i> Lee & Main	+	RE
<i>Heleioporus albopunctatus</i> Gray	n/a	RE ¹
<i>Neobatrachus pelobatoides</i> Werner	+	RE
<i>Crinia georgiana</i> Tschudi	+	RE
<i>Ranidella glauerti</i> Loveridge	+	RE
<i>Ranidella pseudinsignifera</i> Main	+	RE
<i>Ranidella insignifera</i> Moore	n/a	RE ¹
<i>Ranidella subinsignifera</i> Littlejohn	+	LE ²
<i>gen. et sp. nov.</i> Roberts <i>et al.</i>	+	LE
<i>Geocrinia rosea</i> Harrison	+	LE
<i>Geocrinia lutea</i> Fletcher	+	LE
<i>Geocrinia alba</i> Wardell-Johnson & Roberts	+	LE
<i>Geocrinia vitellina</i> Wardell-Johnson & Roberts	-	LE
<i>Geocrinia leai</i> Fletcher	+	RE
<i>Metacrinia nicholli</i> Harrison	+	RE
<i>Myobatrachus gouldii</i> Gray	n/a	RE ¹
<i>Pseudophryne guentheri</i> Boulenger	+	RE

¹ may be found within the boundary of the Warren Bioregion, but only peripherally; reservation status in this bioregion is therefore not applicable (n/a). ² found in the lower south-west, a distribution broadly approximating the Warren bioregion.

Table 4

Summary of the distribution and reservation status of aquatic fauna found in the Warren Bioregion. Number of species found, thus far, in nature reserves (A-class) or national parks within the region are shown in parentheses.

Taxa	Species ¹	Locally Endemic	Regionally Endemic	Widespread
Invertebrates	156	10 (9)	49 (41)	97 (80)
Amphibians	22	6 (5)	13 (13)	0
Fish ²	14	1 (1)	9 (9)	4 (4)

¹ fully described species only; ² native species only.

the inclusion of new reserves to ensure adequate representation of relictual habitats should be an urgent task.

Are the fauna protected in the reserve system?

National parks and nature reserves provide a refuge for a substantial proportion of the aquatic fauna. Their protection, however, cannot be assured unless on-reserve management procedures and activities outside the reserve system are sympathetic to the preservation and maintenance of their habitat.

The practice of conducting fuel reduction burns during late spring, summer and autumn, when the soil is dry, may inadvertently threaten some aquatic fauna either directly or through the loss of soil as habitat. Species such as *L. salamandroides* overwinter in the moist substrate of peatlands and shrublands (Pusey 1990), while other species deposit drought resistant eggs. These organically-rich soils burn readily and hence the fauna within the substratum may be lost. In addition, there may be changes in local hydrology, such as the creation of more surface pools, or improved drainage of sandy soils, which alter the proportional occurrence of habitats and some aquatic species.

Activities occurring within catchments of conservation reserves may impact adversely on the fauna. Harvey (1996) noted that Poorginup Swamp, within the Lake Muir Nature Reserve, was threatened with increased salinization as a result of nearby agricultural clearing. The swamp is the type locality for two species of water mite, *Acercella poorginup* and *Pseudohydryphantes doegi*, both of which were thought to be extinct as a result of recent hydrological changes occurring within the swamp (Harvey 1996). The latter species, however, has been found in one other location, within the Shannon River National Park (Horwitz 1994).

Adverse land-use activities within catchments are even more apparent in flowing waters where anthropogenic activity upstream may directly influence downstream habitats (e.g. Walker 1985; Davey *et al.* 1987; Campbell & Doeg 1989). Land clearing for agriculture in Western Australia has resulted in increased salinity (Schofield 1990) and sedimentation (Williams 1992) of many rivers and clear-fell logging which occurred in the last decade is still affecting streams today (Growth & Davis 1991; Trayler & Davis, *unpubl. obs.*). A river and stream zone system was introduced into the State Forest in the mid-70s (Anon 1977). This was later modified and today this system is estimated to include some 63 100 ha of land in the southern forest region (Anon 1992a). In addition to increasing the size of the conservation estate, these zones of undisturbed vegetation are designed to act as a buffer and minimize the effect of logging operations on the water quality of nearby streams and rivers (Anon 1992a). Large buffer zones (100 m) have been proven effective in reducing the input of sediment into second order streams (Borg *et al.* 1987), but the effectiveness of smaller zones (20-30 m), which are routinely used on these streams, has not been assessed in Western Australia. While there is ample evidence to suggest that these buffers may prevent increased sedimentation (Davies & Nelson 1994; Clinnick 1985), it is unlikely that

such small buffers would prevent increases in stream salinity. Borg *et al.* (1987) found that even 100 m buffers would not prevent a rise in salinity in streams adjacent to logged coupes. There is, however, some evidence to suggest that a large buffer will reduce the period that salinities remain elevated from fifteen years, as estimated by (Borg *et al.* 1988), to eight years, as documented by Growth & Davis (1991). In the past, rising salinity has not been considered important in high rainfall areas where salinities in logged catchments generally remain within the range considered acceptable for drinking water (Anon 1992b). There is, however, increasing evidence that the invertebrate fauna of this region may be intolerant of relatively small increases in salinity (Growth & Davis 1991; Trayler & Davis, *unpubl. obs.*).

The river and stream zone system plays an important role in the conservation of the endemic invertebrate fauna of lotic origin. Many of these fauna have, thus far, not been found elsewhere in the conservation estate (Table 1) and it is therefore essential that riparian buffer zones adjacent to logging coupes are of an adequate size and that these areas are managed properly. Growth (1992) argued that these buffer strips would be compromised if poorly constructed roads or accessways crossed streams to access coupes. In addition, the headwater streams within the karri forest often comprise low gradient, marshy areas with ill-defined and ephemeral water courses which may not be recognised or mapped as first-order streams. There is, therefore, potential for these areas to be overlooked and not included as part of the stream reserve system.

Translocated and exotic fish species are widespread in the waterways of the south-west with increasing anecdotal evidence that these introduced species have a serious impact on the distribution of the native fish fauna (see Morgan *et al.* 1996). Of particular concern is the translocation of piscivorous species such as the golden perch *Macquaria ambigua* and the silver perch *Bidyanus bidyanus* to private dams within the catchment of the D'Entrecasteaux National Park (Morgan *et al.* 1996). These species might further restrict populations of the native fishes if they were to escape into natural waterways.

The non-aestivating native fish species, *N. balstoni*, *Galaxias occidentalis*, *G. munda*, *Edelia vittata* and *Bostockia porosa* are particularly vulnerable to predation by introduced fishes during summer and autumn dry periods when they are forced to retreat to permanent pools and streams (Morgan *et al.* 1996). With the exception of *N. balstoni*, all of these species as well as the lamprey *Geotria australis*, were once found in abundance in the headwaters of Big Brook near Pemberton (Pen *et al.* 1988, 1991), but today their numbers have declined dramatically (Morgan & Gill 1996). In particular, *G. munda*, which was once extremely common to the system (Pen *et al.* 1988, 1991), has now disappeared upstream of the dam and this has been attributed to the recent introduction of the voracious and piscivorous redfin perch *Perca fluviatilis* to Big Brook Dam (Morgan *et al.* 1996).

Big Brook Dam also provides an ideal habitat and potential refuge for a number of other predatory species including *Salmo trutta*, *Gambusia holbrooki* and

Oncorhynchus mykiss (Morgan *et al.* 1996), whose presence may have also adversely affected the native fish fauna in the Big Brook area. While this is yet to be documented for the Warren Bioregion, elsewhere these fishes have been widely implicated in the fragmentation of fish distributions (*e.g.* Tilzey 1976; Lloyd 1990; Hutchinson 1991; Cowl *et al.* 1992).

A variety of other anthropogenic activities and threatening processes operate within nature reserves in the region. Road building activities and the construction of fire breaks, or scrub rolling for fire suppression, increase the likelihood of sediment deposition into wetland systems and enhance the potential for the spread of soil borne fungal pathogens. The effects of these activities have not been fully documented to date.

Recommendations

Conservation reserves within the Warren Bioregion in south-west of Western Australia play an important role in the protection of both the endemic and cosmopolitan aquatic fauna of the entire south-west. The wetlands within these reserves are important refuges for aquatic invertebrates, fishes and amphibians and will become increasingly so as the pressure of urbanisation and agriculture intensifies. Priority for further reservation should be given to aquatic habitats which are known to support a high level of endemic or relictual fauna. It should, however, be acknowledged that the presence of rare fauna is often difficult to detect, and unique faunal assemblages may occur in many of the undisturbed and unsurveyed wetlands of this region. Thus, all relatively undisturbed aquatic habitats in this region should be afforded some protection, at least until they have been properly surveyed.

Since aquatic habitats do not exist in isolation, they cannot be protected within a reserve system without reference to activities occurring within the catchment. Adverse impacts can arise through land clearing, the construction of dams, the introduction of exotic fishes, habitat removal, salinization, sedimentation and eutrophication associated with agriculture, mining, logging and road construction. Careful planning, which is sensitive to the fragility of aquatic habitats, as well as adequate buffers between anthropogenic activities and reserves are essential for the preservation of the fauna in this region.

The effectiveness of a reserve system is also dependent on adequate management within the reserves themselves, where it is essential that due consideration be given to the habitat requirements of the aquatic fauna. This is particularly important for aquatic environments which may be dry for six months or more each year. Seasonal and ephemeral waterbodies must be recognised as comprising an important part of the diversity of aquatic habitats and the absence of water in these environments does not necessarily preclude the presence of aquatic fauna.

Differences between management policy and practice can lead to detrimental effects on aquatic environments (see Davies & Nelson 1994). The environmental awareness of workers carrying out management procedures may be improved through training

specifically in ecological and environmental issues. This important aspect of the management of natural areas currently receives little attention.

Finally, we cannot afford to be complacent with respect to the conservation of the aquatic fauna. Although reserved lands within the Warren Bioregion are extensive, these areas may not be protected in perpetuity. This has been demonstrated by the recent excision of land from the D'Entrecasteaux National Park, near Lake Jasper for the potential purpose of sand mining.

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Ecosystem dynamics and management in relation to conservation in forest systems

R J Hobbs

CSIRO, Division of Wildlife & Ecology, LMB 4, PO Midland WA 6056

Abstract

Any system of conservation reserves sits within the context of the surrounding ecosystem. Modifications to this surrounding matrix will inevitably have some impact on the reserve system. While forest ecosystems in south-western Australia are significantly less modified than other ecosystems, particularly in the agricultural area, they are nevertheless subjected to marked human-induced modifications. These take the form of forest management practices including timber harvesting and fuel reduction burning, and the impacts of introduced species including the pathogen *Phytophthora cinnamomi*. The level of information available to assess the impacts of these modifications is for the most part inadequate. Changing ideas on the nature and dynamics of ecosystems require a reappraisal of how we manage ecosystems for conservation and production purposes. The recognition of interconnections between different impacts and between different ecosystem components has resulted in the development of the concept of "ecosystem management". This aims to integrate the various management goals and allow production to take place in such a way that both the long term productive potential and the biodiversity of the forest are maintained.

Introduction

While there is currently considerable debate over the selection of reserves within forests in Australia, less attention has been paid to how these reserves are likely to fare within the context of the forest ecosystem as a whole. I argue here that conservation reserves do not form discrete entities which can be considered and managed separately from the rest of the forest. Rather, the whole forest has to be considered as a collection of interacting parcels of land, and events in one parcel are liable to impact those in surrounding areas. This has three major implications. Firstly, reserves must be managed not only to meet the needs of the biota being conserved, but also in the context of the main ecosystem processes prevailing in the forest. Secondly, the impacts of management activities in the forest as a whole have to be assessed. Finally, the interconnected nature of natural systems means that the forest as a whole, including those areas outside conservation reserves, plays a vital role in the overall conservation of biodiversity. I explore these points in this paper, and discuss their implications for forest management, with particular reference to Western Australia.

Ecosystem dynamics

The forest ecosystem consists of the forest biota and its environment (Fig 1). The biotic components are divided up according to their primary functions (*i.e.* primary producers, consumers, decomposers *etc.*). These, and other non-living components (dead organic matter, inorganic material) form pools within which

carbon, other nutrients, water and other important elements accumulate. Ecosystem dynamics describe the flows of energy and elements into and out of the system, and between the various pools (*e.g.* Waring & Schlesinger 1985; Aber & Melillo 1991). In addition, the responses to, and recovery from, disturbance form a further important set of ecosystem dynamics, incorporating the ideas of succession and resilience.

Ecosystem processes have frequently been ignored in conservation management, presumably because conservation has been primarily directed at species and biotic communities. Ecosystem ecology has largely developed separately from population and community ecology, and has tended to subsume biotic components into larger "black boxes" (Aber & Melillo 1991), as illustrated in Figure 1. While population and community

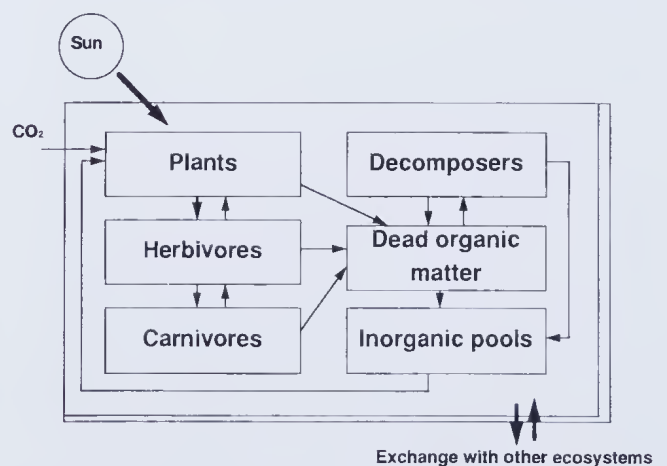


Figure 1. A simplified representation of an ecosystem, indicating the major pools and flows of carbon and nutrients.

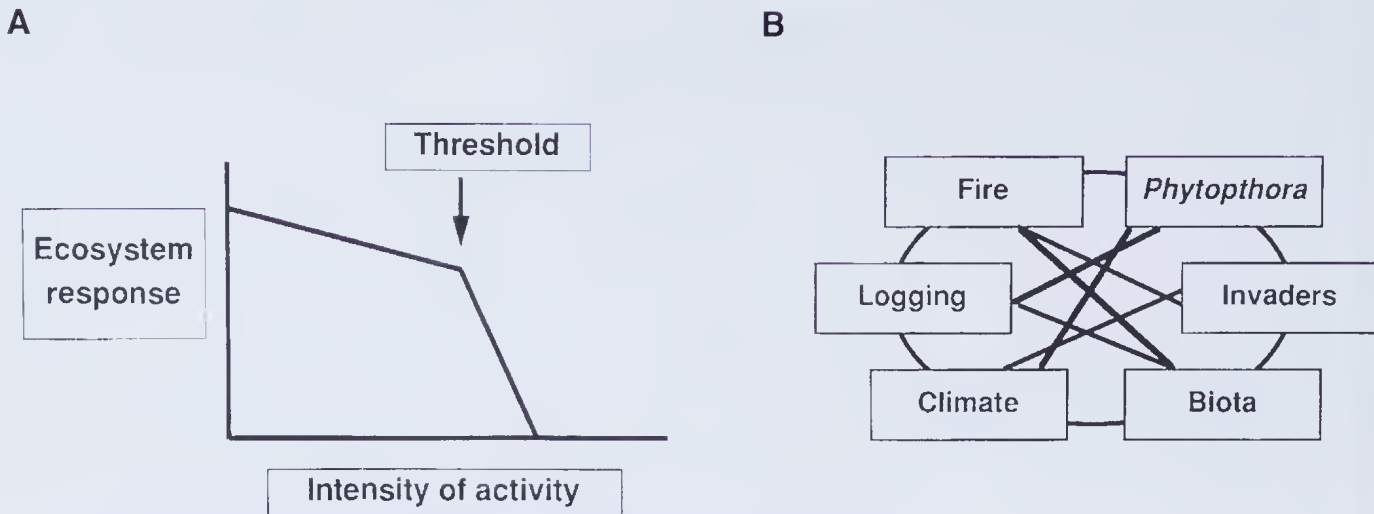


Figure 2. Characteristics of complex ecosystems which render the search for simple cause and effect relationships difficult. **A** Non-linear system response to human activities. The system may show little or no response until a certain level of impact is experienced, at which stage a sudden system change occurs. **B** Complex interactions between system components and human activities. The diagram shows the main factors discussed for Western Australian forest, and potential linkages between them.

ecology have been concerned with entities such as species and populations, ecosystem ecology is concerned with the flows of materials between components - what Pickett *et al.* (1994) have termed the "things versus stuff" dichotomy. However, it is increasingly recognized that the links between species and ecosystems are important, and attempts are now being made to integrate the two streams of ecology (Pickett *et al.* 1994; Jones & Lawton 1995).

In forest systems of Western Australia, the major ecosystem dynamics to be considered include the natural dynamics of the forest, and a set of dynamics imposed by humans. Here, natural forest dynamics are determined largely by three factors which predominate in the area *i.e.* a mediterranean-type climate, with its well-defined summer drought; soils with low nutrient status; and the incidence of fire and other disturbances. These factors, and ecosystem responses to them, have been considered in detail elsewhere (Kruger *et al.* 1983; Dell *et al.* 1986; Dell *et al.* 1989; Davis & Richardson 1995), and I will not dwell on them here. Rather, I will concentrate on the set of imposed dynamics. The most

important of these are forest management practices, in particular timber harvesting and fuel reduction burning, and the impacts of invasive species, including the introduced pathogen, *Phytophthora cinnamomi*.

Introduced species

Phytophthora cinnamomi is undoubtedly a major factor influencing the forest ecosystem in Western Australia and in other parts of the country (Dell & Malajczuk 1989). A recent symposium has highlighted the impacts of the disease on a variety of forest components (Withers *et al.* 1994). From an ecosystem perspective, the disease is important because of its impacts on forest structure and composition and resulting environmental changes. Depending on the severity of attack, *Phytophthora* causes the loss of overstorey and understorey plant species, which then presumably alters the microclimate and reduces evapotranspiration. This in turn leads to increased input of water to the system, which has been recorded as increasing stream flows with increasing degrees of dieback incidence (Fig 3; Schofield *et al.* 1989). This change in local hydrology could potentially lead to localized vegetation change (Davidson 1994), but this has not been investigated in detail.

Introduced predators, particularly foxes and cats, are thought to be one of the major causal factors leading to the complete or near extinction of many Australian marsupials (Burbidge & McKenzie 1989; Friend 1990). Indeed, Western Australian forests have provided the last refuge for a number of species, presumably because fox numbers remained lower than in other areas, and/or they arrived later. Predator control is now practiced in many areas, with obvious success indicated by increases in abundances of native mammals (Kinnear *et al.* 1988; Friend 1990). Changes in abundances of mammals in ecosystems are liable to have impacts on other system components due to their herbivory, digging activities and dispersal of fungal spores (Lamont *et al.* 1985; Noble 1993; Lamont 1995). Such interactions

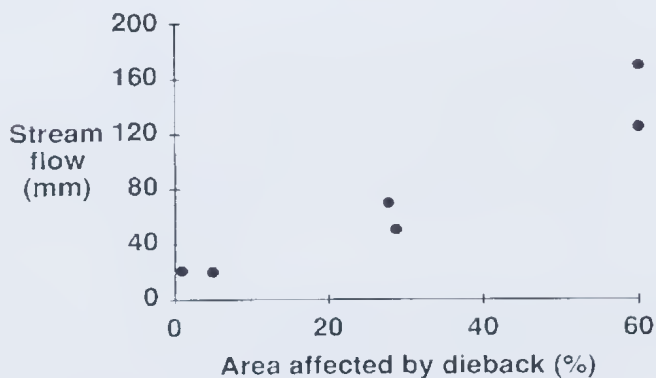


Figure 3. Streamflow in catchments with different proportions affected by *Phytophthora cinnamomi* (redrawn from Schofield *et al.* 1989).

and their disruption may have important, but difficult to detect, effects on ecosystem function (Hobbs *et al.* 1995).

Invasive plants are another major threat to many ecosystems across Australia (Humphries *et al.* 1991; Humphries 1993). Individual invaders, such as bridal creeper (*Myrsiphyllum asparagoides*), have the potential to crowd out native species and alter vegetation composition and structure. Herbaceous species, especially grasses, also have the potential to alter fire regimes by changing the structure and availability of fuel (D'Antonio & Vitousek 1992). In the region of 1500 species are currently naturalized across Australia, with 1032 species recorded from Western Australia (Keighery 1995). Two hundred and twenty species are recognized as noxious weeds across Australia (Parsons & Cuthbertson 1992), and many are problems in native ecosystems. In addition to existing problems, there are likely to be many more species which could become a problem in the future (Hobbs 1993a). These include, for instance, pine species planted in native forest areas which have been found to be invasive elsewhere in the world (Richardson *et al.* 1994). Australia continues to import plant species without due consideration for the potential threats of invasiveness. There is a clear need for an integrated approach to weed management in the forests and elsewhere (Hobbs & Humphries 1995).

Forest management practices

Opinions vary as to the extent to which current forest management practices affect ecosystem processes (Abbott & Christensen 1994; Calver *et al.* 1996). A repeated assertion is that there is no evidence to show that the ecological processes that maintain the forests have been impaired or that forest biodiversity is impacted by forest management (Abbott & Christensen 1994; Anon 1994). However, this may be partially due to the lack of monitoring and research into such potential impacts. In most parts of Australia, little research work has been conducted into the long-term impacts of timber or burning operations. The impact of disturbance-causing activities concentrates on individual species, and no long term monitoring has been implemented, apparently because it is "very difficult" (Anon 1994, p52).

This then leads to a dearth of information with which to assess statements on the impacts of management operations. For instance, Schofield *et al.* (1989) stated that "No long term detailed studies on the effects of different silvicultural systems on the hydrology of the jarrah forest have been carried out". This situation is being redressed (Stoneman 1993), and some information is available from other studies. These indicate that timber harvesting can lead to increases in streamflow over a period of years. Streamflow increases of 91-182% were reported by Borg *et al.* (1987) following heavy logging, and Bari *et al.* (1994) have shown marked increases in streamflow and groundwater discharge following clear felling. These impacts were highest immediately after logging, but persisted for at least 8 years. These findings concur with experimental work carried out elsewhere (Bormann & Likens 1981).

Impacts of logging on other system components are equally poorly documented. What, for instance, are the

impacts of timber harvesting on the nutrient pools in the forest? There are indications from forests elsewhere that impacts on soil properties can be substantial (Rab 1994). While findings from one forest type are not necessarily directly applicable to another, such results indicate that efforts should be made to assess possible impacts in Western Australian forests. Considerable effort has been expended in Tasmania, for instance, in assessing impacts of logging systems on system components (e.g. Hickey 1994; Taylor & Haseler 1995) and clear recognition of the need to consider impacts of management on biodiversity are evident in management manuals (Taylor 1991; Anon 1993; Duncan & Packham 1994; Jackson & Taylor 1994). Little of this type of assessment has been carried out in Western Australia. Work by Mawson & Long (1994) has suggested that current logging practices significantly alter habitat suitability for some bird species, although the validity of the methods used has been questioned by Burrows *et al.* (1995). Similar discussions on the impacts of logging have occurred in Victoria, where Attiwill (1994a,b) has implied that logging is in many ways equivalent to natural forest disturbance, a conclusion which has been contested (Lindenmayer 1995; see also subsequent response by Attiwill 1995).

A similar story is apparent when the impacts of fire management are examined (Williams & Gill 1995). The jarrah forest is currently subjected to widespread short-rotation fuel reduction burning, which has been developed to reduce the risk of destructive wildfires. Controversy surrounds the questions of whether such a burning regime is effective and whether it has adverse impacts on the forest ecosystem (McGrath 1985; Tingay 1985; Underwood *et al.* 1985). It has been claimed that the current regime mimics the regime prevailing prior to European settlement (Burrows *et al.* 1995), although the evidence for this is not compelling. Burrows *et al.* (1995) state that fire scars on *Eucalyptus marginata* trees indicate the occurrence of moderate to severe fires in the forest occurred with a mean interval of 81 years. They then use historical accounts of aboriginal burning and lightning records to conclude that these severe fires must have been accompanied by low intensity fires every 2-5 years. The question remains as to whether such a regime of low intensity fires prevailed over the whole forest or was restricted to areas most frequented by aborigines. If it prevailed over the whole forest, this then suggests that high intensity fires are possible even under a regime of fuel reduction burning, as currently practiced. Indeed, observations in other forest systems suggests that intensive fuel reduction measures do not necessarily "fire proof" forests (DellaSala *et al.* 1995).

Abbott & Christensen (1994) suggest that the current fire regime (and logging activities) are "...a minor, irregular and relatively insignificant perturbation...". On the other hand, McCaw & Burrows (1989) conclude that "While many studies have examined the effects of one, or occasionally several fires, on plant and animal communities in the forest, the basis for predicting longer term effects of different fire regimes is limited". Indeed, the impact of one fire may be minimal, although even this conclusion is open to question (e.g. Majer & Abbott 1989). Again, evidence from Victoria points to a potentially detrimental impact of fuel reduction burning (Hamilton

et al. 1991), although the conclusions of this study again have been questioned (McCaw 1993). Nevertheless, it is the overall fire regime (*i.e.* frequency, intensity, season, size *etc.*) which shapes the vegetation in the long term, and long-term data on vegetation changes under current fire management practices are not available.

Analyses such as that by Abbott & Christensen (1994) look at relatively short time scales and suggest no significant ecosystem changes. For instance, the present fuel reduction fire regime has been in place for less than 40 years, a short time span in terms of forest dynamics. Longer term impacts could be significant, but will not be noticed if relevant monitoring systems are not in place. Even if impacts are detected, it could be some considerable time before a policy or management response is implemented. A clear example of the types of lag involved in responding to problems is the salination of agricultural land caused by past land clearance. This problem was first documented in the 1920s (Wood 1924) but is only now being acted on at the policy level.

Complexity and non-linearity

The degree of debate over the importance of changes to forest ecosystems arising from management practices indicates the difficulty in reaching conclusions on the issue. The problem is further compounded by two characteristics of natural systems. The first is the likelihood that system components exhibit non-linear responses to particular activities (Fig 2A). In other words, the system may change unpredictably or may show relatively little change in response as the intensity

of an activity increases, until a threshold level is reached, at which point system behavior changes dramatically. Alternatively, the system may show no response to a particular activity for a period of time, and then change rapidly. Such non-linear behaviour is a recognized characteristic of complex systems (*e.g.* Roberts 1994).

The second characteristic is the complexity of interactions between system components and processes (Fig 2B). This may be referred to as the "ECWEE" principle *i.e.* "everything is connected with everything else" (see Oppenheimer 1995). While this may be an over-generalization, it is nevertheless the case that complex interactions and feedback loops are common in natural systems. Classical scientific approaches to environmental questions attempt to deny the importance of these interconnections since they render the search for simple cause-and-effect relationships almost impossible. Certainly, much can still be gained by single factor studies, but failure to recognize the potential for complex interactions between factors can also lead to simplistic and misleading conclusions. For instance, while there has been a considerable body of research on the various individual components in Figure 2B, the possible interactions have received little attention. Are there, for example, interactions between the effects of forest management and the spread of *Phytophthora*?

An important part of the problem, however, lies in the continued assertion that current management practices are having little or no impact, even in the absence of data (Abbott & Christensen 1994). It is clear that all management has some impact on the ecosystem (even if the management is to do nothing). The



Figure 4. North Bungulla nature reserve in the Western Australian wheatbelt, illustrating the location of the reserve within a greatly-modified agricultural matrix. Although less obvious, forest reserves also sit within an altered matrix. (Photograph by Dion Steven).

important question is whether the level of impact is acceptable or not. The acceptability or otherwise of any particular impact will change as society's expectations and priorities change. It is clear that forest managers need to be responsive to such changes (Gordon 1994). However, the acceptability of the level of impact can be assessed only if the relevant information is available. In 1977, the Senate Standing Committee on Science and the Environment (Anon 1977) stated that *"the extreme lack of knowledge on the biological sphere.....is hampering responsible decision making"*. In 1993, the Resource Assessment Commission (Anon 1993) still had to conclude that *"the level of information on impacts appears insufficient for most current uses"*. This is echoed internationally by the US National Research Council (Anon 1990), which concluded that *"... the existing level of knowledge is inadequate to develop sound management practices"*. Obtaining this knowledge for Western Australian forests is problematic in the face of current underfunding for research within state agencies and in an environment which is not conducive to open scientific debate on forest issues.

Ecosystem management

How is all this relevant to the selection and management of conservation reserves? Surely it could be argued that impacts in the parts of the forest managed for production are irrelevant if adequate areas are set aside for conservation? Unfortunately, it is becoming increasingly recognized that this is not the case, and that conservation management and production management have to be integrated to achieve the goal of sustainability. Biota and ecosystem processes do not respect legal boundaries (Newmark 1985), and different parts of the landscape interact. Reserves are located within a surrounding altered or managed matrix. This dichotomy between reserve and matrix is obvious in cases where the matrix is noticeably altered, for instance in an agricultural situation (Fig 4). In these situations, there are clear impacts of the surrounding matrix on the remnant vegetation within reserves (Saunders *et al.* 1991; Hobbs 1993b; Hobbs 1994). In the case of forests, the impacts are less obvious, because forestry operations do not necessarily create an entirely transformed matrix. Nevertheless, modifications outside reserves can have impacts within the reserves, and reserves are not immune from factors arising in the surrounding matrix, such as dieback, fire, feral animals and so on.

At the same time, it is also becoming recognized that reserve systems will not be sufficient on their own to conserve the biodiversity of a region, and that conservation and production management have to be integrated to achieve the goals of sustainability and conservation. For instance, Sample *et al.* (1993) suggest that *"Many ecologists agree that neither our current system of forest reserves... nor any conceivable such system will be sufficient to provide adequate protection of biodiversity"*. They continue, *"We are urged .. to consider all lands within the ecosystem as important to its overall functioning and sustainability"*. Further, they suggest, *"We are also urged...to discover ways in which the protection of biodiversity ... can be thoroughly incorporated into the management of lands for a variety of uses and values"*. In

other words, we need to ensure that the areas set aside for conservation sit in a matrix which is managed in a way which ensures the continued integrity of the reserves and provides some conservation benefit as well as productive outputs. This includes forests both on public and private land, especially where private holdings constitute a relatively large component of the conservation and production resource (e.g. Braithwaite *et al.* 1993). Attempts to develop this approach are being made in many different types of forest (e.g. Hansen *et al.* 1991; Caraher & Knapp 1995; Frumhaff 1995).

Such a suggestion could be viewed as an attempt by those interested in conservation to grab as much of the forest as possible and prevent further productive use. On the other hand, it seems likely that continued productive output also strongly depends on the maintenance of healthy, functioning forest ecosystems. The challenge is to find management regimes that optimize both conservation and production and retain the functionality of the ecosystem. Is this a pipe dream? A suggested approach to these challenges is what has been termed *"ecosystem management"*. This approach to management tries to develop a holistic framework and move away from the fragmented and frequently contradictory practices conducted in parts of the forest managed for different goals. Ecosystem management recognizes that a variety of scales are important in management, from the individual site to the landscape and regional scale, and that management needs to be coordinated across these scales (Franklin 1993; Salwasser *et al.* 1993). Ecosystem management also recognizes a key set of ecosystem characteristics, outlined by Costanza (1992), Norton (1992) and Grumbine (1994) :

1. *Dynamism*. The classical idea of the "balance of nature" is being replaced by the concept of the "flux of nature"; i.e. ecosystems are constantly changing and should not be regarded as static entities (Botkin 1990; Pickett *et al.* 1992);
2. *Relatedness*. The "ECWEE" principle discussed above, and the need for cross-boundary management;
3. *Hierarchy*. The idea that natural systems and processes are nested, and the importance of managing at the right scales and recognizing connections between scales;
4. *Creativity and ecological integrity*. Natural systems are self-organizing, and the processes which maintain this organization need to be maintained; and
5. *Differential fragility*. Systems vary in their resilience and thus have to be managed accordingly, as no one prescription will be suitable across a range of ecosystems.

Gordon (1994) and Grumbine (1994) suggested the following principles of ecosystem management:

1. *Manage where you are*. Emphasis on site-specific properties, and the objectives of the management;
2. *Manage with people in mind*. Management needs to consider human desires, influences and responsibilities. Human values play a dominant role in determining management goals. In addition, Sample *et al.* (1993) suggest, *"An ecosystem ap-*

proach must be not only ecologically sound but also economically viable and socially responsible" and "A focus on biophysical factors, with little or no consideration of social and economic needs, is doomed from the start". Magerum & Born (1995) also point to interaction with stakeholders and the public as a key operational component for integrated management;

3. *Manage across boundaries.* The recognition and management of neighbouring influences, and integration of management goals through inter-agency cooperation. Decision support systems and allocation modelling procedures can be used to facilitate this (e.g. Ive & Cocks 1989; Kilgour & Lau 1994)
4. *Manage based on mechanisms rather than "rules of thumb".* Use existing knowledge on processes and interactions, and seek to improve this knowledge. Assume that current knowledge is provisional and be prepared to adapt management practices in the light of new information; and
5. *Manage without externalities.* Include all known components and interactions when management decisions are made.

The goal of ecosystem management, according to Gordon (1994), is a "sustained forest", which exhibits a "full range of characteristics and organisms, not just a sustained supply of wood". Achieving this will not necessarily be easy. There will undoubtedly be problems with definitions and operationalising these definitions (e.g. Burroughs & Clark 1995). The whole concept of ecosystem management requires detailed knowledge of ecosystem processes and often, as discussed above, this knowledge is lacking. This lack of knowledge cannot, however, be used as an excuse or rationale for inaction or for ceasing current practices. Rather, management practices need to be adaptive and experimental, and adequately monitored. Changes in practice should be implemented as more and better information becomes available. However, current management philosophies and structures are not necessarily malleable enough to incorporate the necessary changes in approach. For instance, Sample *et al.* (1993) have suggested that "Another challenge is the reorganization of resource-managing organizations, both public and private, away from function-based, target oriented hierarchies towards open organizations conducive to multidisciplinary approaches to achieving desired future resource conditions".

This problem has been discussed more generally by Holling (1995), who suggests that "The very success of managing a target variable for sustained production of food or fiber apparently leads inevitably to an ultimate pathology of less resilient and more vulnerable ecosystems, more rigid and unresponsive management agencies, and more dependent societies". He sees the underlying causes of this to be the prevalence of a single target and a piece-meal policy, a single scale of focus (typically on the short term and the local), no realization that all policies are experimental, and rigid management with no priority to design interventions as ways to test hypotheses underlying policies. An obvious corollary is that the way to deal with the problem is to reverse these causes, and to develop an integrated cross-scale management policy

and an adaptive management strategy which monitors the impacts of management activities and modifies the regime where necessary (Gunderson *et al.* 1995).

Conclusions

The selection and design of nature reserves and reserve systems is but one part of the strategy required for adequate protection and maintenance of biodiversity in forest ecosystems (or any other type of ecosystem). Reserves sit within a matrix of lands managed for purposes other than nature conservation. While they may be treated as separate legal or administrative entities, they are not separate in ecosystem terms. Ecosystem flows ensure that reserve systems are connected to the surrounding matrix, and the integrity of the reserves is in large measure dependent on what happens in that matrix. The best reserve system in the world will not do what it is supposed to do in the long term if the surrounding matrix is degrading. The surrounding matrix of production lands thus plays a part in maintaining the biodiversity of a region. We thus need to move away from a piece-meal approach to management in which conservation and production management are considered separately. Management goals are now much more complex than previously and aim to maintain not only a sustainable harvest of timber, but also the structure and complexity of the forest ecosystem. The concept of ecosystem management aims to integrate the various management goals and allow production to take place in such a way that both the long term productive potential and the biodiversity of the forest are maintained. The challenge is to make the concept operational and to convince everyone involved of the urgent need to do so.

Acknowledgments: I thank B Main, D Spratt, R Wills and two referees for constructive comments on the draft manuscript. Part of this paper appeared previously in the Proceedings of the Symposium "Professional Forestry: Evolving Issues in Forest Management", 1996, School of Forestry, University of Christchurch, New Zealand.

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Forest reservations: an overview

A R Main

Zoology Department, University of Western Australia, Nedlands WA 6907

Abstract

This paper is placed in the context of the assumptions made when suggesting criteria for selecting areas for reservation. It is suggested that, in the absence of detailed taxonomic knowledge, site selection might be improved by recognising the possibility that relict occurrences of past environments will include equally ancient biotic assemblages. Moreover, the reasons for the persistence of such past environments offer guide-lines for management which will ensure their retention.

Introduction

When I was first asked to provide an overview for this Symposium the proposed title began "Requirements for Reservation....", the latest version is "The design of Reservations". It is easy to see why the title has been changed; to require is to insist upon having. In a biological sense it is broadly known what is required of reservations. But requirement also carries a connotation of asking or claiming by right or authority. So, the latter title is less likely to be misconstrued because design, as a scheme or plan, purpose or intention, is less coloured. The other papers in this issue have embraced these subtleties. In this overview I wish to emphasise the importance of including historically significant biological elements as a requirement of adequate design for reservations, allude to scientific procedures so that non-scientists may understand why interpretations change, and show that historical knowledge of the biota offers a guide for management.

The Commonwealth has proposed a set of criteria for National Forests Conservation Reserves defining forests as woody vegetation with a potential height >5m (Anon 1995:41). In the proposed criteria it is frequently stated that there is a need to emphasise national estate values. Moreover, "*our knowledge of forest species is limited, large numbers of invertebrate species are reasonably presumed to be undiscovered and/or undescribed*" (Anon 1995:24). It is proposed that this deficiency can be overcome by identifying habitats as surrogates for these values. This is in contrast to various studies which suggest that plants and vertebrates are such surrogates, while the Commonwealth position is that consultation and 15% of the original or pre-European extent of forest present will adequately reserve forest communities.

A common approach to the problem is to accept the present as given, then after survey and classification, select areas for reservation *i.e.* assume tomorrow will be like today. Yet other perspectives and procedures on these topics are in terms of whether reserves are adequate, comprehensive and connected. Another possibility is as follows; some of the National Estate

values reside in historic elements of the biota which can be readily recognised. Their occurrence is tied to historical/geological events and land forms resulting from them. Their origins go back to the time when there was only one great southern continent, the land mass known as Gondwana. The plants and animals which survived from this time contribute much to the distinctive character of the biota and sets aside the bioregion as being unique *i.e.* having National Estate values. The aquatic and wetland habitats favoured by animals are readily recognised and thus present themselves as potential surrogates when identifying areas for reservation.

Goals

As a minimum we wish to retain replicated, representative areas of natural biodiversity so that those who come after us may know what the present day world was like. While we are interested in retaining biodiversity, usually conceived as species or genetic richness, within reservations, we need to ask the questions: Is this goal reasonable? Can it be achieved? We cannot foresee the future and can only know the present, so does this give a sound basis for choosing areas or expecting success?

A central question which arises with the goal of conserving through reservation is: will tomorrow (the future) be like today (the present)? *i.e.* will what we know and cherish about nature be able to persist tomorrow? Common sense tells us that today is like yesterday or at least not too different and so common sense suggests that tomorrow will be like today. But in science, common sense is not taken as a good guide; rather, it is a conjecture which must then be subject to rigorous tests to show whether these conjectures are true. Only when repeated attempts at refutation have failed can any faith be placed in the conjectures and the interpretations that follow from them.

The world is neither static nor stable and nature persists in a non-equilibrium state *i.e.* selection and genetic composition of populations or the populations composing communities are the result of past selection and temporary assemblages arising from transient circumstances. But this happened in the past also, so we might conclude that tomorrow will be like today. Espe-

cially so because the same classes of biological interactions will occur, methods of interaction will be similar but rates will be different and the resource base reduced unless we are careful, so tomorrow may not be like today.

The foregoing paints a picture of great uncertainty and is the central issue facing us when selecting areas for reservation and managing them. Management can address uncertainties by adopting a system of adaptive management as advocated. Landscapes rather than reserves might be the management unit. But our concepts of reserve design and adequacy are pitifully incomplete because of the poor and very slowly expanding knowledge base. Additionally, there is the question of whether 15% (or any other arbitrary percentage) of an area can cover the foregoing uncertainties.

Ideally, selection of areas for reservation would follow comprehensive surveys. These are time-consuming, expensive and hindered by inadequate taxonomic expertise. Moreover, the results might not be timely in the sense that for various reasons decisions need to be made before the survey can be completed.

So what is a prudent course of action? The more particular and specific are the goals the greater the likelihood of misjudgement *i.e.* specific goals require detailed knowledge, but this takes an inordinately long time to acquire. However, generality based on understandable principles relating to biological needs of animals of gondwanan origin might be a way of selecting areas. Moreover, the general principles might be confirmed from a knowledge of what happened following changes in the past and might incidentally give guidance for management.

History

Australia is a fragment of a former super continent, Gondwana. Since it broke away some 60 mybp, Australia has traversed 35-40 degrees of latitude and has come from a region with a cool damp climate to the unreliable climate with seasonal drought characteristic of its present low latitude situation. So today is not like yesterday.

The last major sculpting of the western landscape occurred during the Permian glaciation 250 mybp. The subdued landscape that resulted from the glaciation has dominated stream flows and erosion patterns ever since. The current system of salt lakes for example are the relicts of early Tertiary rivers and these in turn may represent Mesozoic drainage channels.

While the drainage channels show their origin they also show the influence of more recent events, such as the sagging of the southern margin of the Western Australian part of the Australian plate as it fragmented from Antarctica and the uplift of the western margin along the Darling Fault and Meckering line. These events changed the direction of streams affected by the tectonic events to either the west or south (Hocking & Cockbain 1990). The nett result was a new cycle of erosion with the head waters of these streams, in some cases, cutting back into the streams of the plateau. More recently, rainfall has become seasonal, and evaporation higher resulting in the accumulation of cyclic salt in the soil profiles in areas of lower rainfall (Ghassemi *et al.* 1995: 155, 180).

From the taxonomic literature it is possible to identify many invertebrate groups which have Gondwanan affinities occur in South East Australia, New Caledonia, New Zealand, South America or South Africa (Main & Main 1991; Hopper *et al.* 1996; Table 4). A field inspection of the localities from which animals have been reported reveals the easily recognised environmental characteristics where habitat favourable for invertebrate animals with Gondwanan affinities may be found. Such sites are damp or wet, often with impeded drainage and showing little or no signs of salinisation. Such sites can be considered to resemble or be representative of habitats which were more widespread in earlier times. Thus with respect to the sites and habitats identified as containing gondwanic elements today is like yesterday and such sites, even without detailed surveys for reservation are likely to retain significant Gondwanan biota

The present

Surface characteristics, drainage, topography and rainfall combine to determine the quality of any water within a catchment. Under high rainfall conditions, soils accumulate little salt while in low rainfall areas salt accumulates in the soil profile and is released as ground water discharge when the hydrological balance is disturbed *e.g.* following clearing. Saline ground waters are common in the semi-stripped etch plain to the north and east of the forest region and absent in the high rainfall areas to the west and south of the region. Thus three sorts of river water occurs, saline in those streams whose head waters drain the semi-stripped etch plain; streams which are saline in the head waters but fresh in the lower reaches where flow from fresh tributaries dilutes the saline waters from the upper reaches; and those, usually short streams, draining only high rainfall areas.

The erosion by the western and southern streams has resulted in the present etched landscape of high topographic relief so characteristic of the high rainfall areas, particularly along the Darling Scarp and in the vicinity of Manjimup and Pemberton (Finkl & Churchward 1973). This new landscape contrasts markedly with the former subdued Gondwanan topography.

To summarise the changes to the present; the latitude of the continent has changed, climate has altered and become more seasonal, and much of the old surface has been destroyed by erosion. To refer back to the introductory analogy, today is not like yesterday. This would suggest simply that biotic relicts of ancient times will not have survived to the present! Yet collection of biotic material quickly shows that this is not so. *Podocarpus* is an obvious example; it has a long geological history from at least early Tertiary times and still occurs in other fragments of the former Gondwana. But there are countless other plant genera with equally ancient lineages *e.g.* *Xylomelum*, *Adenanthos*, *Banksia* and other Proteacea. Many terrestrial invertebrates show their Gondwanan origins through their affinities and relationships to elements of the other southern continents. So, despite the changes noted above there must be some places which are still like yesterday. Some of the sites can be characterised and thus offer a good guide for

selection of areas having a high likelihood of containing Gondwanan elements and thus capable of retaining this element of biodiversity. Moreover, some of the unique vertebrate elements also occur in similar or the same sites e.g. freshwater fish (Hopper *et al.* 1996; Table 4).

The low topography of the old Gondwanan surface and in places on the incipient etch plain results in poor drainage, ill defined water courses, and extensive areas of swamp land which is either permanently wet or variously referred to as winter-wet or summer-dry swamps. These swamp lands provide one of the modern habitats which retain Gondwana-like characteristics. In drier sites invertebrate elements with gondwanic affinities have adapted by modifying life histories e.g. aestivating or behaviourably by burrowing. The chain of soil types (the catenas) of the valley sides, even in saline areas often have a series of summer-dry swamps each with its own characteristic fauna and flora. Better drained areas permit the growth of jarrah and karri which provide a closed canopy and thus another Gondwana-like habitat. Thus each land surface has its own hydrological regime and the potential to retain different Gondwanan elements. The retention of whole catenas with perched swamps and impeded ground water flow extending from granite crests to valley floors is important.

Selection of Gondwanan sites

So, what are the characteristics which could be used to identify sites for reservation so that Gondwanan elements might be conserved (Main & Main 1991; Hopper *et al.* 1996)? They are;

- 1 unaffected by salinisation;
- 2 high rainfall areas with short summer drought;
- 3 topographically high south coastal areas subject to frequent mists, cloud and drizzle;
- 4 areas adjacent to granite rocks from which water is shed;
- 5 areas of impeded ground water flow so producing winter-wet swamps;
- 6 streams with extensive fresh head water swamps and year round flow;
- 7 areas where vegetation can harvest water from fog or cloud by drip from leaves and stem flow e.g. tingle forest and south coast dunes and heath;
- 8 areas with southern or south-western aspect which are thus sheltered from summer insolation e.g. valley slopes and wet valley floors; and
- 9 areas of intact forest canopy under which the characteristic under storey shrubs and herbs occur.

Endemic elements

The foregoing are not the only criteria for selecting elements of the biota for conservation. Numerous plants and animals have evolved since Gondwanan times. Such species will be found in sites whose characteristics have developed more recently *i.e.* are drier, better drained or

more exposed, eucalypts and acacias are perhaps the most successful of these more recently evolved types. But, any sites where evolution and selection might be expected to produce unique endemic forms because they are different to 'typical' Gondwanan land forms should be considered when surveying for conservation sites e.g. the twig-lining habit of the spider *Aganippe raphiduca* (B Y Main 1976). Thus in selecting sites for reservation the following should be considered in addition to those in which old Gondwanan elements may occur;

- a. new topographic elements to which Gondwanan forms may have evolved adaptations and thus become unique endemic elements of the biota; and
- b. sites where Tertiary and more recent migrants to the south-western part of the continent have evolved to be typical elements of certain communities or ecosystems.

Implications

A goal of retaining Gondwanan elements has implications for management. The fossil record shows a long history of fire in Australia. However, many Gondwanan elements, especially wet-land forms, are more sensitive than later evolved forms to fire and so in site selection and management this factor needs to be considered.

Field inspection of sites from which biotic elements with Gondwanan affinities have been collected suggest that in addition to fire, drainage, harvesting or removal of vegetation cover and salinisation are all inimical so management plans that recognise the need to retain special elements and the dangers to their persistence have the maximum chance of ensuring that tomorrow (the future) will be like today (the present).

Recent developments demonstrate the readiness with which the tourism industry will embrace new reservations as a resource to be exploited. Such use has the potential to destroy the qualities which justified the initial reservation. Such an outcome can only be negated by detailed expensive management, or by having numerous large areas reserved, within which there is an adequate and significant replication of historically important habitats.

Nevertheless it should always be borne in mind that reservations will only be part of a mosaic of land uses whether they be within native forests, plantation forests of eucalypts or conifers, or wheatfields. Their health and persistence will be inextricably linked to the whole matrix of reservations, how isolated the biota of each reservation may be and how the management of the non-reserved portion of the landscape impinges on the long term viability of the reservations *i.e.* the landscape rather than the individual reservation is the management unit. This last point is important because large size or an adequate surrounding buffer when areas are selected for reservation may be the only practical way of ensuring their long term viability.

Conclusions

The common practice when selecting areas for conservation reserves is to interpret the broad patterns of

the current situation without any time dimension. A further assumption is that what is present now will persist in the future despite interference and disturbance *i.e.* the future will be like the present. Elsewhere (Main 1996) I have expressed doubts about ecosystem stability and suggested a dynamic state as being a more realistic assumption. Furthermore, there is a strong possibility that increased amounts of greenhouse gases in the atmosphere will result in climatic changes which may impact on this nature conservation estate (Main 1993). Despite these possibilities, ecosystems are in a dynamic state on a trajectory determined by biological responses to environmental changes set in train as the continent moved from high latitude moist equable climates to warmer drier more seasonal ones. In this process the cool climate moisture dependent elements have been restricted to refugia which are usually small scale, long undisturbed, habitats which are easily overlooked in large scale forest harvesting. When selecting areas for reservation to retain biodiversity we should realize that despite an absence of detailed taxonomic knowledge of the cool temperate Gondwanan elements of the biota we do have a basis for selecting reservations so that the possibility of retaining this element of the biodiversity is maximised.

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Volume 80 Part 1
March 1997

Museum of Victoria



43646

ISSN 0035-922X

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Cover design: Mangles' kangaroo paw (*Anigozanthos manglesii*) and the numbat (*Myrmecobius fasciatus*) are the floral and faunal emblems of Western Australia. Also depicted is a collection of living stromatolites which are of particular significance in Western Australian geology. The three subjects symbolize the diversity of sciences embraced by the Royal Society of Western Australia. (Artwork: Dr Jan Taylor).

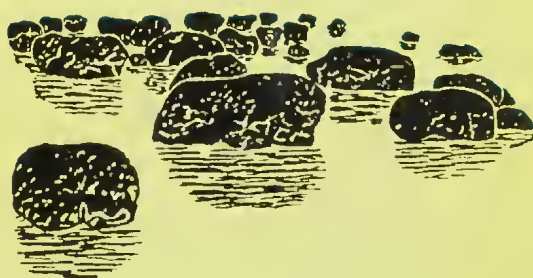
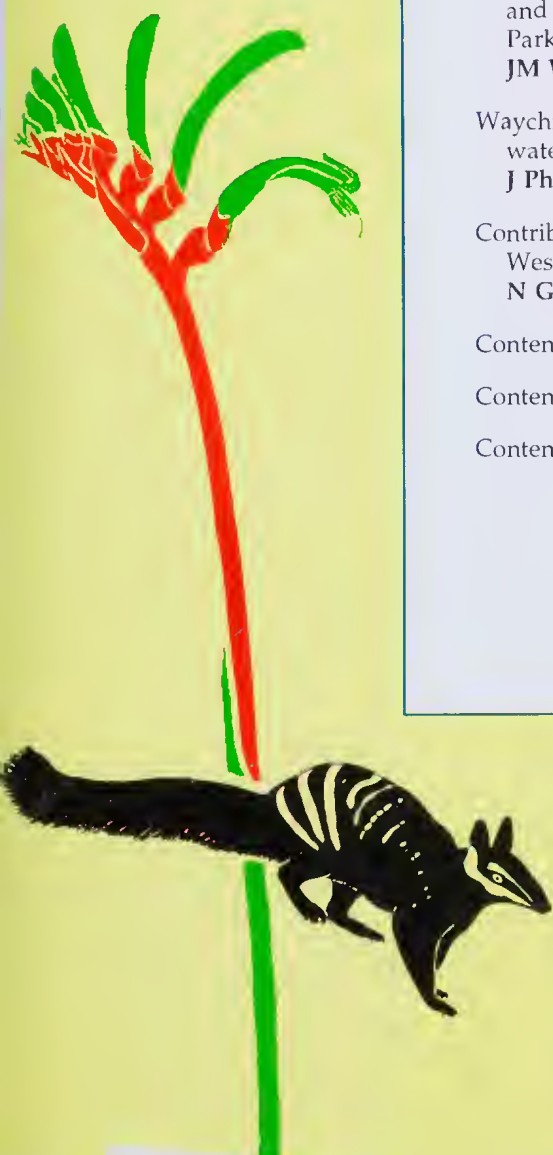


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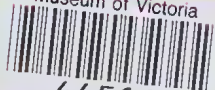
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Museum of Victoria



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ISSN 0035-922X

The Royal Society of Western Australia

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Cover design: Mangles' kangaroo paw (*Amigozanthos manglesii*) and the numbat (*Myrmecobius fasciatus*) are the floral and faunal emblems of Western Australia. Also depicted is a collection of living stromatolites which are of particular significance in Western Australian geology. The three subjects symbolize the diversity of sciences embraced by the Royal Society of Western Australia. (Artwork: Dr Jan Taylor).



Granite Outcrops Symposium September 14-15, 1996

sponsored by
The Royal Society of Western Australia,
The Gordon Reid Foundation for Conservation
The University of Western Australia

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Preface

S D Hopper¹ & P C Withers²

¹Kings Park and Botanic Garden, West Perth WA 6005

²Department of Zoology, The University of Western Australia, Nedlands WA 6907

The Granite Outcrops Symposium was held at The University of Western Australia on September 14 and 15, 1996. It aimed to achieve a cross-disciplinary synthesis of current knowledge on granite outcrops, and to distill effective guidelines for conservation managers.

About 15% of the earth's continents consists of granite, which may outcrop in the form of inselbergs – ranges, ridges and isolated hills – that stand abruptly from surrounding terrain, like islands in a sea. Most commonly, granite outcrops appear as dome-shaped hills with bare rock exposed over much of their surfaces. The water catchment so formed, combined with a diversity of microhabitats, make granite outcrops havens for biodiversity world-wide.

In Western Australia, granite outcrops form characteristic landforms across much of the gently undulating terrain of the State. These granite outcrops are of special interest:

- geologically, being among the world's oldest rocks
- hydrologically, providing a source of water in a dry landscape
- biologically, as refuges rich in endemic plants and animals, and
- culturally, being vital for aboriginal, colonial and contemporary peoples alike.

Despite their intrinsic interest, world-wide occurrence, and special values in Western Australia, granite outcrops had yet to be the subject of a significant cross-disciplinary scientific meeting. For these reasons, the Royal Society of Western Australia decided to host a two-day symposium on granite outcrops, including a combination of invited reviews and contributed papers. Over 70 participants from local, national and international destinations contributed to a diverse and stimulating meeting.

The symposium was significant in high-lighting ideas of global importance concerning the geology, landforms, biodiversity and human use of granite outcrops. Special research opportunities arise from the insularity and geographically compact nature of most outcrops. They offer model systems for exploring evolutionary and ecological processes, and for achieving conservation outcomes through the stewardship of informed local communities.

Participants at the symposium resolved to meet again on publication of these proceedings at a management workshop aimed at helping conserve granite outcrop biodiversity and cultural heritage. In addition, at least two books proposed by invited reviewers are now well underway, receiving extra impetus from discussions at the 1996 symposium. These initiatives alone have affirmed the value and success of the Royal Society of Western Australia's initiative.

Perusal of this volume highlights the diversity of scientific ideas and opportunities deserving future research on granite outcrops. We hope that the symposium will stimulate other contributions to a most deserving field of multi-disciplinary enquiry.

As editors, we thank the Royal Society of Western Australia for hosting the symposium, the Gordon Reid Foundation for Conservation for a significant grant without which the symposium would not have been such a success, and The University of Western Australia for providing a suitable venue for the meeting. Don Edward, our colleague on the organising committee, made an invaluable contribution for which we are grateful.

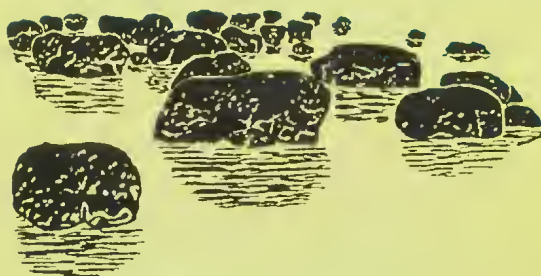
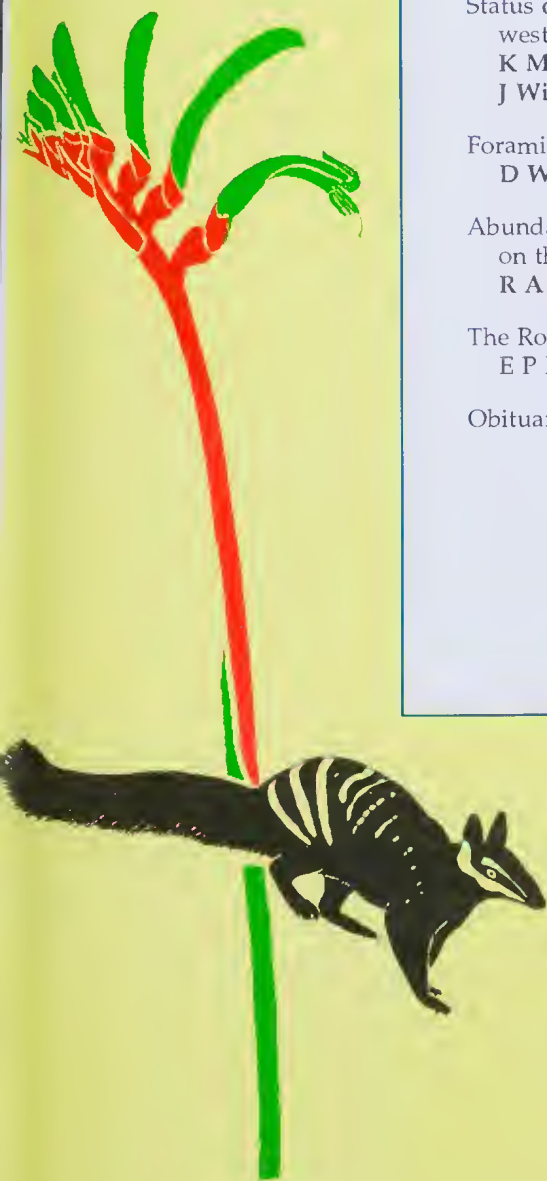


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PREFACE

Mini-Symposium on Satellite Remote Sensing and its Applications in Western Australia

Satellite remote sensing is a rapidly-developing technology which has important roles in many aspects of science, industry and government. It is a particularly important technology in Western Australia with its considerable land mass, extensive coast-line and off-shore waters. Fortunately, the Leeuwin Centre for Earth Sensing Technologies at Floreat Park, and the affiliated institutions and researchers including CSIRO, DOLA, TAFE, Curtin University and World Geoscience Corporation, provide state-of-the-art facilities for local researchers. The Royal Society of Western Australia consequently sponsored a mini-symposium on aspects of satellite remote sensing with particular reference to its uses in Western Australia, by drawing upon the expertise of researchers at the Leeuwin Centre.

The Mini-Symposium on Satellite Remote Sensing and its Applications in Western Australia was held as a monthly meeting of The Royal Society of Western Australia on Monday 18th September, 1995, at the Leeuwin Centre for Earth Sensing Technologies. The meeting was convened by Dr Andy Gable (CSIRO Division of Exploration and Mining), who provided a brief overview and technical background to the different remote sensing technologies. Mr Alan Pearce (CSIRO Division of Oceanography) then presented several case studies concerning the uses of satellite remote sensing in the marine environment. Thermal satellite data provide sea-surface temperature imagery, which is being used in studies of the ocean currents off Western Australia and their role in recruitment to a number of local fisheries, including the western rock lobster, scallops in Shark Bay, and the salmon and pilchard fisheries along the south coast of Western Australia. The images also helped explain the movement of the oilslick from the disabled tanker Kirki in 1991. Use of medium resolution colour imagery for bathymetric and habitat studies in shallow coastal and bay waters, such as Broome, Shark Bay and Geographe Bay, and high resolution imagery for monitoring water quality in estuaries such as the Peel Harvey system, were described. Dr Richard Smith (WA Department of Land Administration) then discussed the uses of satellite remote sensing for land surface structures. Vegetation spectral properties for comparing different vegetation types over space and time can provide information on land productivity and weather events. For example, effects of land clearing on rainfall patterns, movements of flood waters, erosion, and bushfires can be monitored. Dr Ian Tapley (CSIRO Division of Exploration and Mining) described three applications of remote sensing in mineral exploration. SAR (synthetic aperture radar) sensing technology can provide information on surface topography and soil properties, and Landsat images reveal spectral properties of soil related to the surface regolith. Dr Gable then concluded the mini-symposium with a brief look at future technologies and their potential applications.

This issue of *The Journal of the Royal Society of Western Australia* presents two papers based on this mini-symposium and provides a comprehensive bibliography of studies using satellite remote sensing technology with particular reference to Western Australia.

The Royal Society of Western Australia thanks the contributors to the mini-symposium, and Alan Pearce and Richard Smith for preparing papers for this issue of the journal.

Philip Withers
Honorary Editor

Applications of satellite remote sensing to the marine environment in Western Australia

A Pearce¹ & C Pattiaratchi²

¹ CSIRO Division of Marine Research, Marmion WA 6020: alan.pearce@marine.csiro.au

² Centre for Water Research, University of Western Australia Nedlands, WA 6907: pattiar@cwr.uwa.edu.au

Manuscript received February 1997

Abstract

Satellite remote sensing is the only feasible means of monitoring on a regular basis the large expanse of oceanic surface waters off Western Australia, and marine scientists are increasingly applying this technology to studies of our coastal and ocean waters. Up to now, most use has been made of Landsat Multi-Spectral Scanner (MSS) and Thematic Mapper (TM) imagery for studies of estuarine and coastal features, and the NOAA Advanced Very High Resolution Radiometer (AVHRR) for sea-surface temperature and inferred ocean currents. Some preliminary work has also been undertaken on the chlorophyll distribution of our continental shelf waters using the Coastal Zone Colour Scanner (CZCS). Satellite remote sensing will continue to play an indispensable role in marine science with the availability of altimeters for directly monitoring sea-surface elevations (and hence ocean circulation), scatterometers for surface winds and waves and ocean colour sensors for studies of chlorophyll distributions and ocean productivity.

Introduction

Western Australia has a coastline of some 8230 km (excluding offshore islands, which increase the total coastline to about 12330 km; R Galloway personal communication) and the area of the continental shelf is about 400,000 km² (Jarvis 1986). Because of the complexity of oceanic processes on a range of temporal and spatial scales as well as the expense and limited range of research vessels, the only effective way of monitoring such large areas on a regular basis is through remote sensing. For the past decade, marine scientists in Western Australia have effectively applied satellite remote sensing to study our ocean waters, using the imagery to complement oceanographic data collected by conventional (surface-based) methods and to obtain background information for areas where little other data are available.

Satellite remote sensing has appreciably advanced our knowledge of surface oceanic features off Western Australia. Over the next decade, more accurate and higher resolution satellite sensors will play an increasingly important role in marine research, improving our knowledge of ocean circulation, mixing processes, upwelling systems, wave generation, plankton blooms and fish distributions. It must be remembered, however, that remote sensing effectively covers only the surface waters of the oceans, and therefore complements conventional oceanographic measurements of the subsurface structure.

In contrast with the cool equatorward eastern boundary currents in the South Atlantic and South Pacific Oceans, the dominant ocean current along the Western Australian coast is the Leeuwin Current (Godfrey & Ridgway 1985; Pearce & Walker 1991; Smith *et al.* 1991), a warm poleward flow of tropical water (Fig 1). Also unlike the Benguela and Humboldt Current systems,

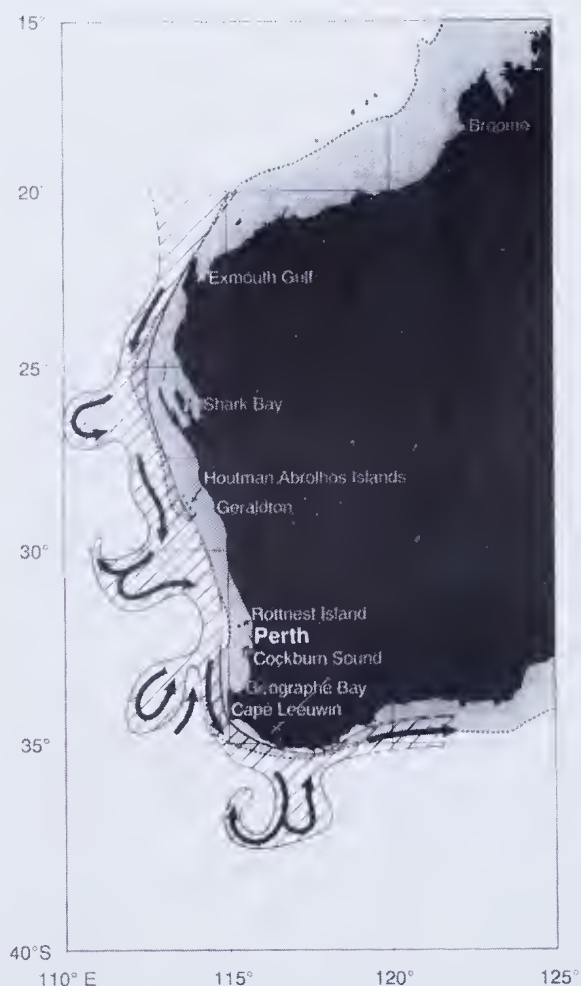


Figure 1. Map of Western Australia showing its marine regions. The cross-hatch area is a schematic representation of the Leeuwin Current, and the dotted line shows the approximate position of the edge of the continental shelf.

there is no persistent upwelling of cool nutrient-rich sub-surface water onto the Western Australian continental shelf, and consequently sea temperatures off Western Australia are significantly higher than at the same latitudes off southwestern Africa and Chile (Pearce 1991). The Leeuwin Current appears to play an important role in the biogeography of the south-eastern Indian Ocean (Maxwell & Cresswell 1981; Morgan & Wells 1991; Hutchins & Pearce 1994) and to influence recruitment to some of the commercial fisheries of Western Australia (Pearce & Phillips 1988; Lenanton *et al.* 1991; Fletcher *et al.* 1994; Caputi *et al.* 1995).

Here we review applications of satellite remote sensing in Western Australian coastal and continental shelf waters, briefly outlining the most important results from published as well as unpublished research. Our aim is to demonstrate both the past use and future potential of marine remote sensing in our State and to illustrate how different remote sensing techniques have contributed to our knowledge of local oceanic processes. Technical details should be sought in the standard oceanographic remote sensing textbooks such as Robinson (1985) and Stewart (1985) and in the companion paper by Smith (1997). Further information on local marine applications can be gained from the extensive bibliography prepared by Smith & Pearce (1997).

Satellite remote sensing

It is less than four decades since the first satellite (the Russian Sputnik) was launched into space in October 1957, to be followed by many earth-observing satellites with a variety of specialised sensors (Fig 2). The "modern era" of oceanographic remote sensing was perhaps born in 1978 when three highly successful satellites were launched; the short-lived Seasat (with a wide array of sensors including an altimeter, synthetic aperture radar SAR and scatterometer), Nimbus-7 (with the Coastal Zone Colour Scanner CZCS) and TIROS-N (carrying the Advanced Very High Resolution Radiometer AVHRR). Satellites may be broadly classified as geostationary (effectively fixed in space some 36000 km above the equator and rotating with the earth) or polar-orbiting.

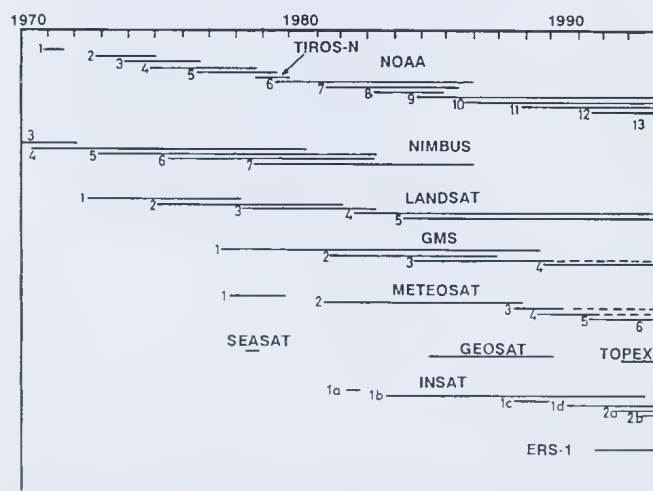


Figure 2. Operational periods of selected satellites useful for marine remote sensing from 1970 to 1993. Dashed lines indicate satellites which are still functional but not currently operational. (See text for details.)

There is a chain of geostationary meteorological satellites viewing almost the entire earth's surface at half-hourly intervals; these include the Japanese GMS satellite (located above the equator at 140° E to the north of Australia), the European Meteosat and Indian Insat. These carry both visible and infrared sensors and are largely used for weather monitoring although they have also been used for oceanographic purposes in some parts of the world.

Polar-orbiters, on the other hand, orbit the earth a few hundred km over the poles with a revisit period of one to a few days, and generally have a higher spatial resolution (smaller pixel size on the surface) than the geostationary series. Many of the polar-orbiting satellites have played a crucial role in oceanography, including the highly successful TIROS/NOAA meteorological satellites (with altitudes around 830 to 870 km and orbital periods of about 102 minutes, first launched in the late 1970s and providing more useful imagery over the oceans than any other series of satellites) and the Landsat series, launched in June 1972 as the first operational high-resolution satellite monitoring the earth's surface and resources. Nimbus satellites generally carried experimental sensor packages which may have then become operational on other satellites. Seasat and Geosat were specialised satellites for monitoring sea-surface topography and roughness, as are the currently-operating Topex/Poseidon and the European Remote Sensing Satellite ERS-1.

There are four basic properties of the ocean which can be measured using the visible, infrared and microwave portions of the electromagnetic spectrum. These are:

- surface temperature, which reveals surface circulation patterns including thermal fronts and upwelling zones;
- water colour, used to measure phytoplankton and other particulates in the water column as well as properties of the seabed, and so assist in the study of ocean fronts, surface circulation patterns, upwelling regions, dispersion of river and outfall effluent plumes, and seabed habitats in shallow water;
- surface elevation, where microwave altimeters measure the distance between the satellite and the sea surface to study ocean circulation and tidal heights; and
- surface roughness, showing surface waves and wind from backscatter caused by wind on the ocean surface.

The first two properties can be measured using passive techniques in which electromagnetic radiation emitted by (or reflected from) the water surface and the atmosphere is received at the satellite sensor. The third and fourth properties are measured by the return of pulses of electromagnetic energy that are actively transmitted from the satellite and the reflected/scattered signals are received back at the sensor.

For larger-scale oceanic studies, such as mesoscale (10's to 100's of kilometres) ocean circulation and monitoring of upwelling zones, the polar orbiters with sensors such as the AVHRR and CZCS (pixel size of order 1 km) are adequate. For coastal waters, where smaller-scale processes are important, sensors such as the Landsat TM with pixel sizes of less than 100 m are appropriate.

We concentrate here on satellite remote sensing of surface temperature and ocean colour in Western Australian waters to illustrate the role that each has played (or is playing) in studying marine systems in this State. Satellite measurements of surface topography and roughness have not yet been used to any extent in our waters but will almost certainly become invaluable tools in the future.

Sea surface temperature

Satellite-derived sea-surface temperature (SST) measurements have been available for over two decades and have been widely used for the derivation of circulation patterns, structure of oceanic fronts, behaviour of eddies/meanders and the location of upwelling zones. The temperature in the upper layer of the ocean is influenced by radiative processes and both incoming and outgoing surface heat fluxes. Vertical mixing usually ensures that the temperature of the thin surface "skin" (from which the infrared radiation is emitted) is close to the "bulk" temperature of the upper few metres of water. Surface temperatures therefore generally reflect the subsurface thermal structure which is in turn related to ocean currents.

SST can be estimated using thermal infrared sensors such as the AVHRR on the NOAA series of satellites, with a pixel size of 1.1 km and a swath width of about 2800 km (Fig 3) and the Thematic Mapper (TM) on

Landsat 4 and 5, which has a single thermal infrared channel with 120 m pixels and a 185 km swath. Two NOAA satellites are maintained operationally at any time, and each passes over any particular place on the earth's surface twice per day. The AVHRR on satellites NOAA-7, -9, -11, -12 and -14 has 5 spectral bands; one in the visible region of the spectrum, one in the near-infrared, a third in the mid-infrared, and two in the thermal infrared. The visible and near-infrared bands are useful in daylight for land/sea/cloud discrimination, and combinations of these bands are used to derive vegetation indices (Smith 1997) and for cloud detection. Techniques of cloud detection are many and varied, but the simplest (and most popular) involve using threshold limits from both individual bands and combinations of bands (e.g. Saunders & Kriebel 1988a, b).

Sea-surface temperatures are computed by combining the radiance temperatures derived from the two individual thermal bands to account for the varying amounts of water vapour in the atmosphere (Barton 1995). Pearce *et al.* (1989) compared AVHRR-SSTs derived from a variety of SST algorithms with surface measurements off Perth and selected the McMillin & Crosby (1984) formulation as giving the most reliable results in this area; this was confirmed by some unpublished data from the Abrolhos Islands, although on occasion the difference between the AVHRR and *in situ* temperatures was found to exceed 2 °C. [More recent unpublished data indicates that better

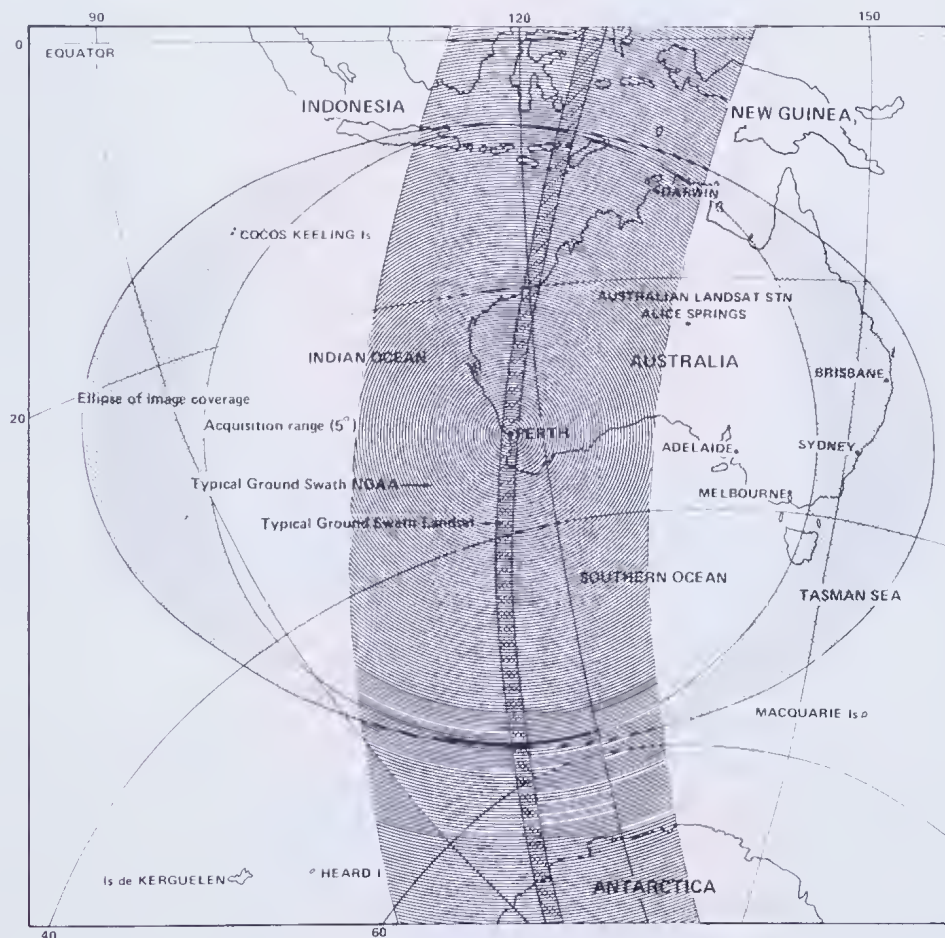


Figure 3. Map of the approximate coverage of a typical swath of the NOAA/AVHRR (broad shaded band) compared with that of Landsat (narrow band) (Carroll 1982). The stippled circle/ellipse indicates the total reception area for the AVHRR from the Perth receiving station.

corrections may in fact be required near the edges of the swath, the so-called "scan-angle effect"]. Pellegrini & Penrose (1986) found that the McMillin & Crosby (1984) algorithm was also appropriate for tropical waters of the Northwest Shelf, but they suggested that scan-angle effects may become important towards the edges of images in such regions with high water-vapour loadings.

Western Australian satellite users are fortunate that the first AVHRR receiving station in Australia was established in Perth in 1981 (Carroll 1982) as a joint project between CSIRO and the Western Australian Institute of Technology (now Curtin University). AVHRR satellite images from satellites NOAA-6 to NOAA-14 have been archived in Perth since late 1981, the longest AVHRR archive in Australia (Pearce 1989) which is being used extensively in studies of the Leeuwin Current and its interaction with inner-shelf waters.

NOAA/AVHRR: Large-scale circulation and the Leeuwin Current

Historically, the earliest use of SST imagery off Western Australia appears to have been a study of thermal conditions on the Northwest Shelf in 1966 by Szekielka & Mitchell (1972), who used High-Resolution InfraRed (HRIR) imagery from the Nimbus-2 satellite to derive the annual cycle of SST. They also pointed out the presence of anomalously warm patches of water in this region of high air-sea heat flux. Prata & Lynch (1985) and Lynch *et al.* (1986) further examined these patches (which can have a horizontal scale of 200 km and are up to 2° warmer than the surrounding water) and deduced that they can propagate southwestwards at over 1 m s⁻¹. This is too fast for normal advective processes, so it was concluded that the patches are possibly caused by spatial and temporal variations in localised heating/cooling of the near-surface waters.

While earlier studies of ocean temperatures and salinities had shown a seasonal change in water properties off Western Australia (Rochford 1969; Gentili 1972), current trajectories from free-drifting buoys as well as hydrographic measurements led to the identification and naming of the Leeuwin Current (Cresswell & Golding 1980). The advent of NOAA/AVHRR imagery received in the United States in the late 1970s provided the thermal resolution to confirm the strong southward transport down the west Australian coast during the autumn and winter months and the much weaker flow in summer, also revealing details of the complex eddy-like features associated with the Leeuwin Current (Fig 4; Legeckis & Cresswell 1981).

Since the establishment of the NOAA receiver in Perth in 1981, locally-received AVHRR imagery has become a well-used tool in studies of the structure and variability of the Leeuwin Current and associated coastal waters off Western Australia. The surface temperatures show the Leeuwin Current as a strong current meandering southwards from about Exmouth along the edge of the continental shelf; on reaching Cape Leeuwin, it curves eastwards and flows into the Great Australian Bight.

Along both the west and south coasts, however, satellite (Prata *et al.* 1986; Pearce & Griffiths 1991) and drifting buoy (Cresswell 1980) studies have shown that the Leeuwin Current is in fact a complex of mesoscale (order of 100 km) eddies and meanders interposed with along-

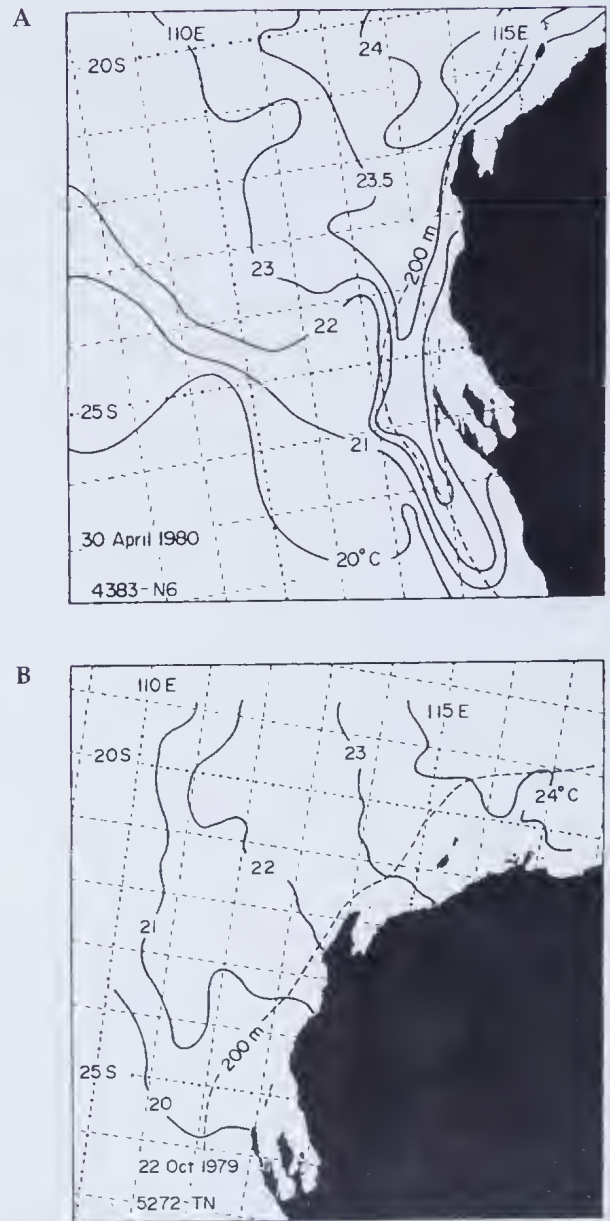
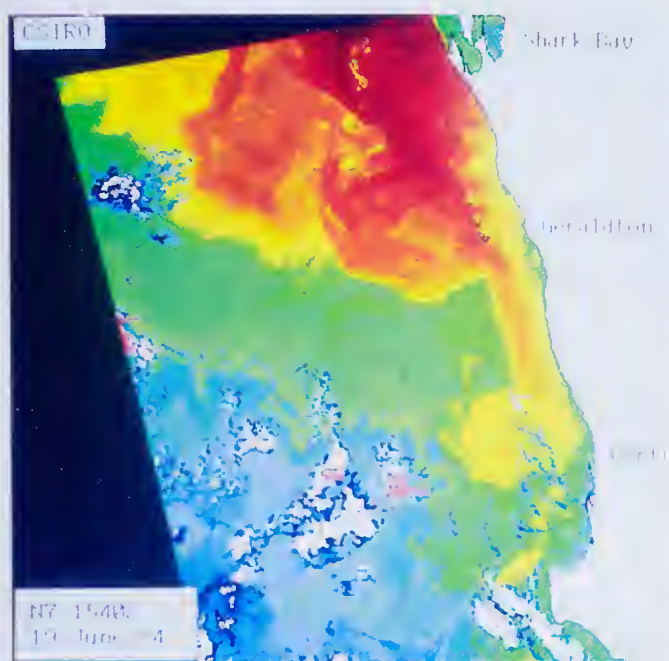


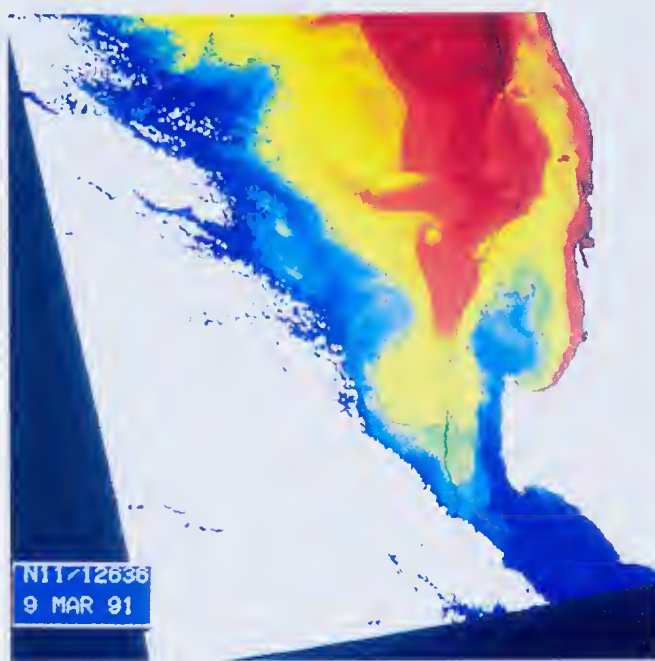
Figure 4. Sea-surface temperature contours off Western Australia. A: April 1980, the tongue of warm water penetrating southwards along the outer continental shelf showing a strongly-flowing Leeuwin Current. B: October 1979 with a weak current. Reprinted from Deep-Sea Research Volume 28, Legeckis R & Cresswell G R, Satellite observations of sea-surface temperature fronts off the coast of western and southern Australia, pages 297-306. Copyright 1981. With kind permission from Elsevier Science Ltd, The Boulevard, Langford lane, Kidlington OX5 1GB, UK.

shore current jets. There are frequently a number of these wave-like meanders of different dimensions along the west coast, deflecting the Current offshore and representing an active transport of warm Leeuwin Current waters into the southeast Indian Ocean (Plate 1). These anti-cyclonic (anti-clockwise) meanders can grow to more than 200 km from the coast on occasion before apparently becoming unstable and either breaking off as free-standing eddies (Griffiths & Pearce 1985a) or simply dissipating. Between the meanders, strong alongshore current jets stream southwards along the shelfbreak and outer continental shelf.

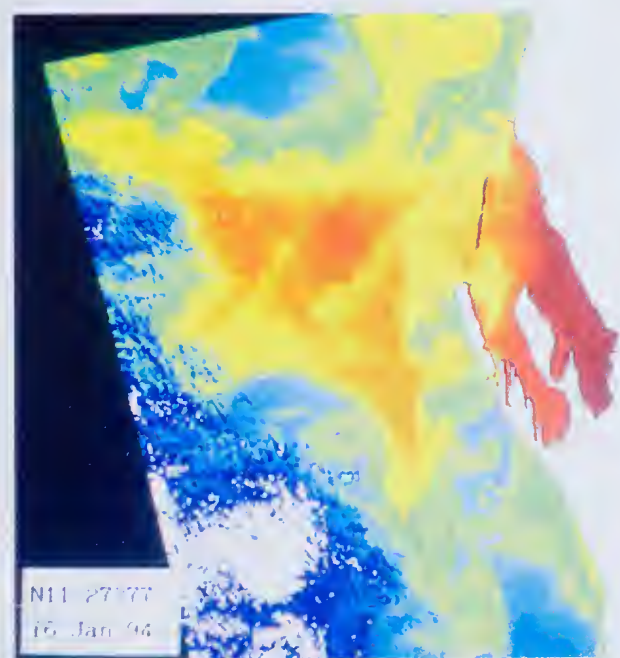
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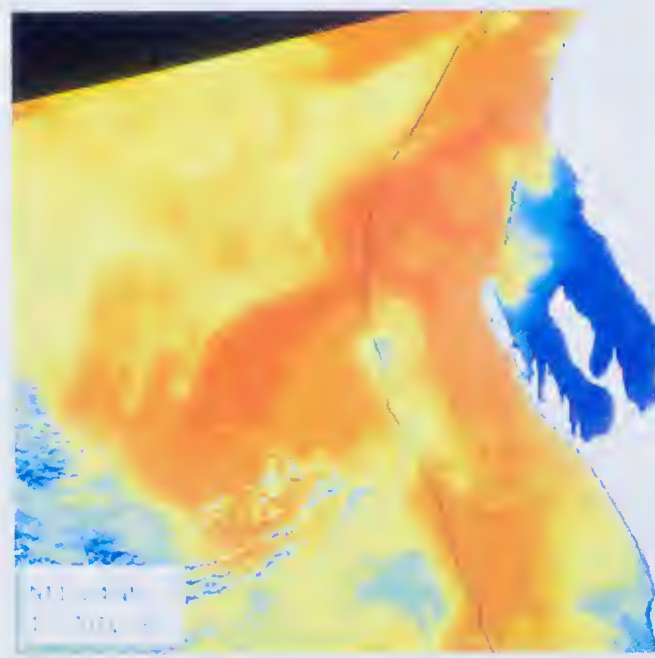


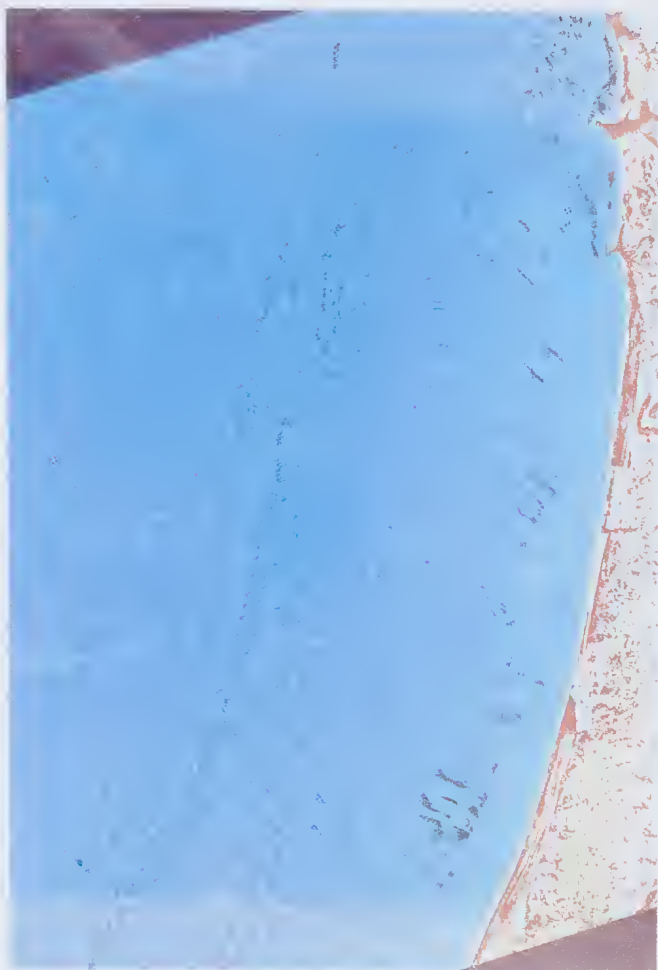
Plate 1. NOAA-AVHRR image of the Leeuwin Current between Shark Bay and Cape Leeuwin in June 1984. The image has been geometrically corrected and shows the brightness temperature in band 4, with warmest water (the Leeuwin Current) in red cooling through yellow and green to the coldest water in blue. Land is white and clouds are mottled blue/white. Image received by the Western Australian Satellite Technology and Applications Consortium.

Plate 2. NOAA-AVHRR image of the cool Capes Current flowing northwards off south-western Australia in March 1991. Other details as in Plate 1.

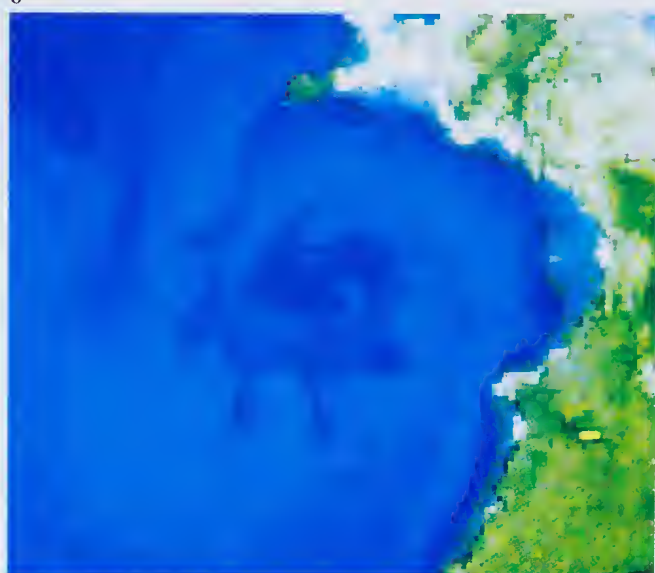
Plate 3. NOAA-AVHRR image of Shark Bay; January 1994, representing summer conditions. Other details as in Plate 1.

Plate 4. NOAA-AVHRR image of Shark Bay; July 1993, for winter. Other details as in Plate 1.

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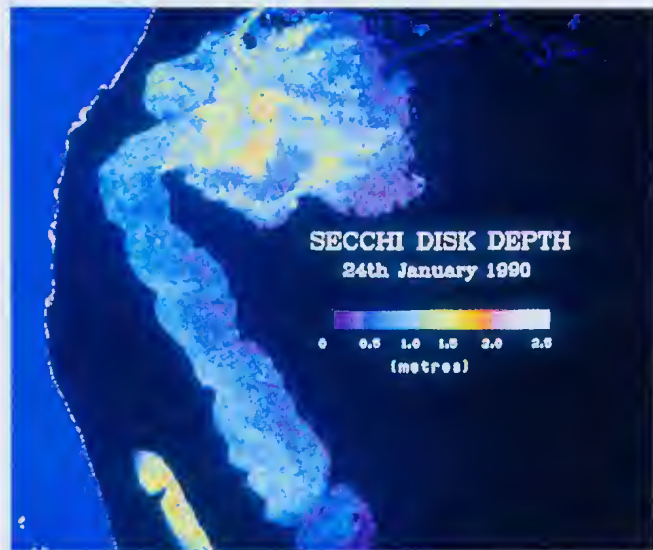


Plate 5. Bathymetry off Broome derived from a Landsat TM Band 1 image in December 1987. The image shows bottom stratigraphic features, the two features parallel to the coast in the middle of the picture being in water depths of 15 to 30 m. (Image courtesy of Peter Hick, CSIRO).

Plate 6. Wake eddy behind Cape Voltaire (14° 16' S, 125° 35' E) in Admiralty Gulf, enhanced from a Landsat TM image. The horizontal scale of the eddy is about 1 km in a current of about 1.5 m s⁻¹.

Plate 7. Landsat TM image of the Peel-Harvey estuary, showing the equivalent of Secchi disk depth on 24 January 1990, derived from a combination of Landsat TM bands 1 and 3. Reprinted by permission of the Publisher, from Lavery P S, Pattiaratchi C B, Wyllie A & Hick P T, Water quality monitoring in estuarine waters using the Landsat Thematic Mapper, Remote Sensing of Environment Volume 46 pages 268-280. Copyright 1993 by Elsevier Science Inc.

Plate 8. Landsat MSS composite image (bands 4, 5, 7) of the Capes area on 14 November 1984 (courtesy Alex Wyllie and Robert Shaw, WA Department of Land Administration) showing internal waves near Cape Leeuwin.

Closer inshore, there is a seasonally-varying northwards counter-current along the continental shelf north of Rottnest Island (Cresswell *et al.* 1989). However, satellite images have suggested that a cold plume also penetrates northwards past Cape Leeuwin during the summer months (Phillips *et al.* 1991; Cresswell & Peterson 1993). More detailed analysis of a series of AVHRR images enabled Pearce & Pattiaratchi (unpublished observations) to define and name the Capes Current, a nearshore current flowing northwards past Capes Leeuwin and Naturaliste and along the mid-continental shelf past Rottnest Island. In contrast with the winter situation where the Leeuwin Current is close inshore near Cape Leeuwin, the Leeuwin Current swings offshore in summer as the Capes Current penetrates northwards against the coast (Plate 2). This cool current (which may also involve localised upwelling; Gersbach *et al.* personal communication) is narrow and shallow, persisting between about October and March while the wind stress is strongly northward.

After rounding Cape Leeuwin, the Leeuwin Current changes character. In contrast with the meandering behaviour along the west coast, where the current path as a whole deflects offshore, the current along the south coast tends to run along the outer continental shelf (with the strongest currents just beyond the shelfbreak) towards the Great Australian Bight. It is characterised by strong thermal fronts as the tropical water borders cold Southern Ocean waters. Periodically, warm offshoots peel off to the south and temporarily disrupt the eastward flow (Griffiths & Pearce 1985b; Cresswell & Peterson 1993); these features frequently have the form of eddy pairs, with clearly-defined clockwise (cool) and anticlockwise (warm) circulation elements. Some offshoots continue

growing southwards away from the coast and eventually separate from the Current to drift away as freely-rotating eddies 300 km or more offshore (Griffiths & Pearce 1985a).

Using AVHRR imagery to complement simultaneous Acoustic Doppler Current Profiler (ADCP) measurements from a research vessel, the three-dimensional structure of the Leeuwin Current and some of the warm offshoots can be analysed. Cresswell & Peterson (1993) measured current velocities in some of the offshoots which were evident in satellite images, finding current speeds of up to 1.5 m s^{-1} (Fig 5). This work is a fine example of the value of linking conventional oceanographic measurements with satellite imagery.

By extracting digital SST transects across the Leeuwin Current from the imagery, the surface expression of the current structure can be quantified in terms of the position of the peak temperature in the current and derivation of SST gradients (Prata & Wells 1990; Pearce & Griffiths 1991). The thermal topography varies seasonally and with latitude. During the summer months when the Leeuwin Current is weak, the thermal structure is ill-defined and SST gradients are small, but significantly increase while the current is strengthening in autumn, before decaying again in late spring (Pearce & Prata 1990). As the Leeuwin Current flows southwards into increasingly cool waters, the temperature differential across its boundary correspondingly increases. At the latitude of Shark Bay, this differential is typically about 1° C , whereas off Perth it is more like 2° to 3° C and along the western part of the south coast where the warm Leeuwin Current waters enter the Southern Ocean it can exceed 4° C (Godfrey *et al.* 1986; Prata & Wells 1990).

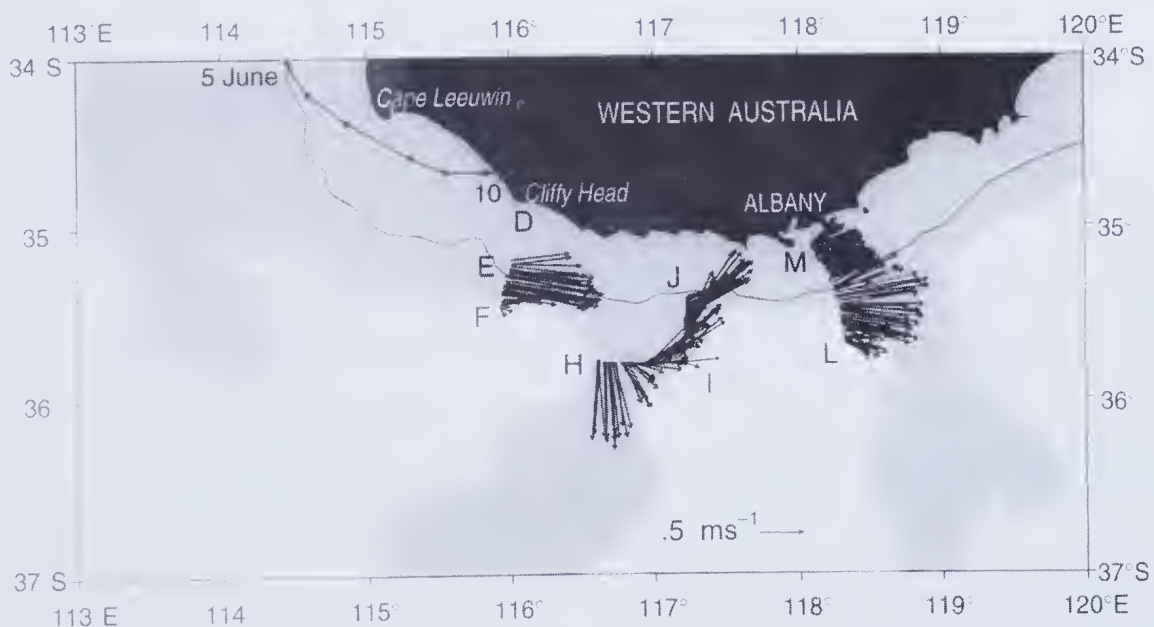


Figure 5. Surface currents in Leeuwin Current offshoots along the south coast near Albany. The shaded region represents warmer water from a NOAA-AVHRR image and the current vectors are from the ADCP (see text). The letters D to L are from the original paper and are not used here. Reprinted by permission of the Publisher from Cresswell G R & Peterson J L, The Leeuwin Current south of Western Australia, Australian Journal of Marine and Freshwater Research Volume 44 pages 285-303. Copyright 1993.

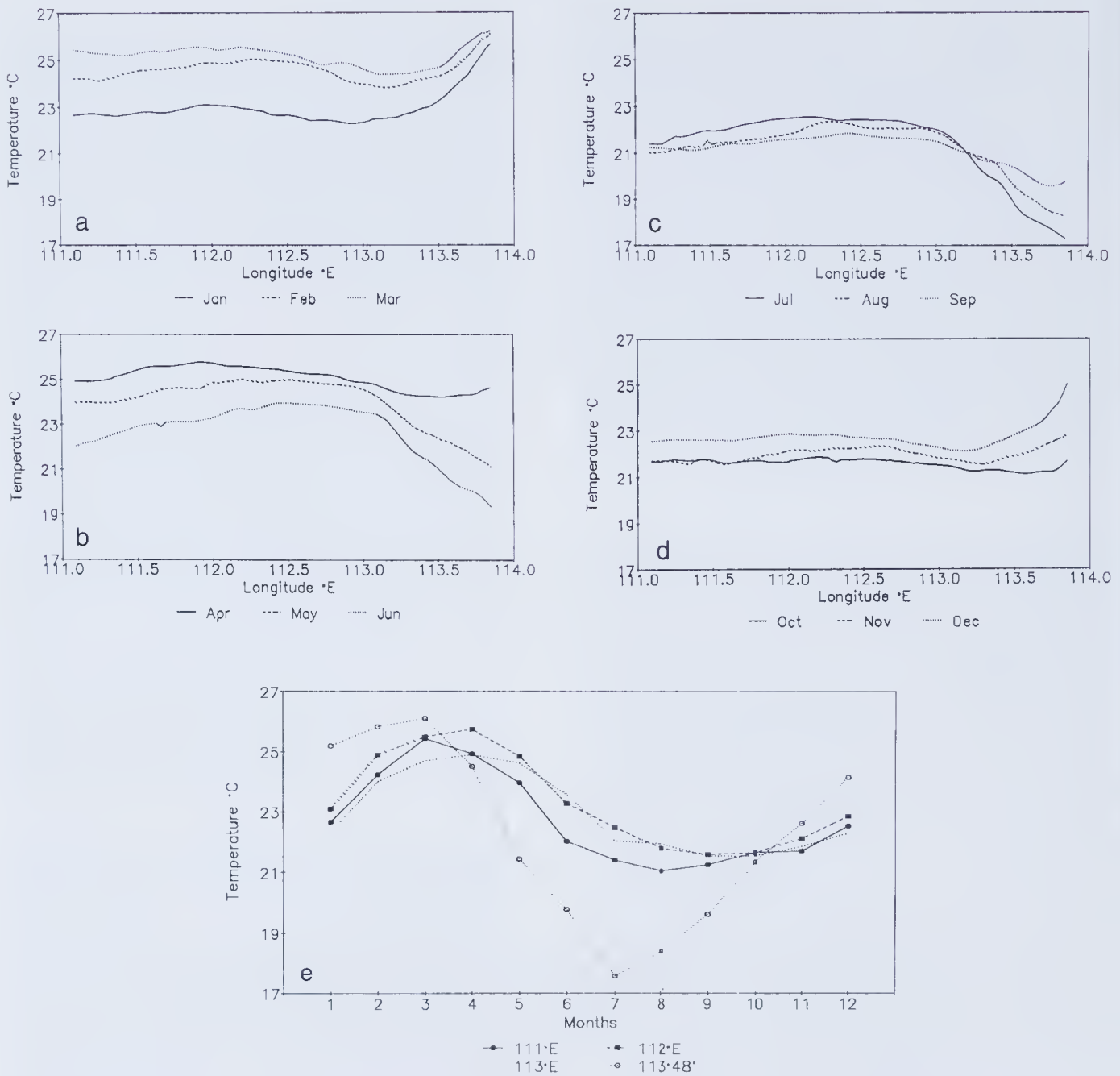


Figure 6. A to D Monthly mean SST transects on latitude $25^{\circ} 20' S$ across the continental shelf between $111^{\circ} E$ and the eastern shore of Shark Bay derived from AVHRR data 1988 to 1993. E: depicts the seasonal SST cycle at four selected longitudes representing offshore water ($111^{\circ} E$), the Leeuwin Current ($112^{\circ} E$), the entrance to Shark Bay ($112^{\circ} E$) and the shallow eastern part of Shark Bay ($113^{\circ} 48' E$).

Prata *et al.* (1986) derived the trajectory of the Current by determining the position of the peak SST along each dataline, clearly illustrating the meandering of the flow down the coast.

Another example of digital data extracted from AVHRR imagery is a series of monthly mean SST transects across the continental shelf at $25^{\circ} 20' S$ and extending into Shark Bay, illustrating the seasonal variation in cross-shelf thermal structure. In the summer months (Fig 6A, Plate 3), the water near the eastern shore of Shark Bay is 3° to $4^{\circ} C$ warmer than that outside the Bay. During autumn and into winter (Plate 4; Fig 6B, C), the shallow water in the bay cools as heat is lost to the

atmosphere so that by June the eastern bay water is $4^{\circ} C$ cooler than that in the Leeuwin Current. As spring extends into summer, the cross-shelf gradient switches again (Fig 6D). The transition months when the water is almost isothermal across the shelf and Bay are April and October. The seasonal variation is graphically shown in Figure 6E where both the amplitude and phase of the annual cycle change between offshore and the bay itself; in the Leeuwin Current ($112^{\circ} E$) the water is warmest in May and coolest in September/October and the annual range is $4^{\circ} C$, whereas in the eastern bay ($113^{\circ} 48' E$) the range is almost $9^{\circ} C$ and the extremes are in March and July.

NOAA/AVHRR for fisheries applications

Because of anticipated links between water temperatures and fish catches (particularly for pelagic species such as tuna), one of the original motivations for establishing the NOAA remote sensing facility in Perth was to provide SST imagery to the fishing industry. A study examining the correlation between satellite-derived SSTs (provided in real-time to the fishing industry) and southern bluefin tuna catches along the southwestern coast of Australia (Myers & Hick 1990) found somewhat inconclusive results. This was largely because of the inadequate facilities available for image acquisition and processing at that time, persistent cloud over the fishing area near Albany, the general decline of the tuna stock (with consequent changes in the operation of the industry) and the practices of the fishermen themselves. Nevertheless, recent improvements in both the reception and image processing facilities have enabled SST images to be made available to the fishing industry in real-time, and some fishing companies in Western Australia are now making use of the pictures to assist in fishing management decisions.

To explain some of the established links between the flow of the Leeuwin Current (as indexed by annual mean coastal sea levels) and recruitment of the western rock lobster, Pearce & Phillips (1988) have suggested that the strong onshore flow in the southern part of mesoscale meanders may regionally boost the shoreward migration of the phyllosoma larvae. A particularly well-defined meander in an AVHRR image during the settlement period in October 1984 may have contributed to exceptionally high local settlement at Dongara at that time. Likewise, AVHRR images suggested that fluctuations in recruitment at Cape Mentelle (34° S) may be associated with the onshore/offshore position of the Leeuwin Current in that area (Phillips *et al.* 1991).

The annual recruitment of tropical fish larvae at Rottnest Island in April has been attributed by Hutchins & Pearce (1994) to the southwards flow in the Leeuwin Current. Analysis of AVHRR imagery indicated that the arrival of larvae was associated with tongues of Leeuwin Current water penetrating across the shelf to bathe the Island, although the authors acknowledged that other factors (both oceanographic and biological) would certainly play a role as well.

Fletcher *et al.* (1994) used AVHRR images to assist in the interpretation of pilchard larval and egg distributions along the south coast. Larval surveys during the July spawning period when the current flows most strongly showed that there was eastward advection of eggs and larvae along the shelf at between 30 and 40 km d⁻¹ (35 to 45 cm s⁻¹). During the December spawning, on the other hand, there was no indication of alongshore advection of eggs and larvae because the current is weaker at that time of year.

AVHRR imagery also proved useful in explaining the movement of an oil slick from the tanker Kirki which lost its bow near Jurien in 1991, with fears that the oil spill could decimate the sensitive rock lobster nursery reefs. Analysis of SST images shortly after the disaster showed that a meander of the Leeuwin Current was responsible for carrying the oil offshore despite generally onshore winds at the time. Use of current patterns derived from

the imagery in OSSM (the On-scene Oil Spill Model) enabled the oil distribution to be reproduced in the model (Easton *et al.* 1992), proving the value of satellite imagery in marine disasters of this type.

NOAA/AVHRR and submerged strandlines

In a novel use of AVHRR thermal imagery, Tapley (1990) produced a relief-shaded night-time image of surface thermal boundaries for a coastal region off Broome. Oceanic eddies were revealed, but more surprisingly the image also showed the surface expression of submerged limestone strandlines consisting of pairs of narrow ridges some 300 to 500 m wide and rising 5 to 8 m above the seabed in water about 20 m deep. Tapley's interpretation was that the strandlines created vertical currents and both the upwelled cooler water and changed surface sea-state were evident as a thermal signature. The presence of the strandlines was verified by diver observations during the validation phase of the study.

NOAA/AVHRR for coastal processes

While the mesoscale meanders and eddies described above extend offshore (westwards), smaller eddies and billows with length scales between 5 and 35 km are also found along the inshore boundary of the current and penetrate across the continental shelf (Pearce & Griffiths 1991; Wyllie *et al.* 1992). Field studies of nearshore oceanographic processes off Perth using conventional oceanographic measurements complemented by NOAA-AVHRR and Landsat TM imagery have revealed some of the dynamics of the interaction between the Leeuwin Current and the nearshore waters (Mills *et al.* 1992). Cross-shelf mixing processes result in active "flushing" of the inshore region and are believed to play a role in the dispersal of coastal pollutants. A composite TM image also showed discoloured water from the Peel-Harvey estuary and the Swan River moving northwards (Wyllie *et al.* 1992), illustrating the complementary roles of multi-spectral and multi-scale imagery in interpreting coastal and nearshore processes.

Nevertheless, under appropriate conditions NOAA/AVHRR imagery alone can reveal relatively small-scale localised features, such as upwelling around Rottnest Island caused by the interaction between flow and topography ("island wake effect"). During the summer months, the predominantly southerly winds drive the currents on the continental shelf northward past Rottnest Island, resulting in a persistent cold water patch immediately to the north of the Island (Pattiaratchi, unpublished data). During winter, on the other hand, interaction between the southward flowing Leeuwin Current and Rottnest Island leads to flow separation with the formation of an eddy off the western tip of the Island.

Another coastal application of full-resolution thermal AVHRR imagery involved a tidal jet from an estuary at Bunbury (Hearn & Pearce 1985), showing a plume of buoyant warm water extending some 5 km from the inlet, with a maximum thermal contrast of about 0.5° C; this is approaching the limits of the radiometric and spatial resolution of the AVHRR sensor. Estimates of the frontal propagation speed and entrainment coefficient using the image and a tidal model agreed with those obtained using surface measurements.

Ocean Colour

In contrast with thermal infrared remote sensing, comparatively few ocean colour data are available for Western Australian continental shelf waters, because the CZCS was operational only intermittently and because the visible band on the AVHRR has insufficient spectral resolution to adequately detect the small range of colour changes in the open ocean. For coastal waters, however, remote sensing in visible wavelengths has been used for monitoring chlorophyll (phytoplankton) concentrations, suspended sediments, and bottom type (in clear shallow water). Visible imagery is, of course, only useful during daylight hours and in cloud-free conditions.

While thermal infrared energy is emitted from a thin surface skin, water-leaving radiance in the visible region of the spectrum indicates colour variations in the upper part of the water column, depending on the absorption, reflection and scattering of sunlight from particles in the water as well as on surface illumination, roughness, foam and surface films. Clearly, the spectral characteristics of a water body depend markedly on the mix of phytoplankton species present, the ages of the various components and the presence of inorganic particles. Because much of the radiance reaching the satellite is from scattering and reflection by the atmosphere, corrections must be applied to remove these atmospheric components from the water-derived upwelling signal.

The colour sensors which have been most widely used are the Multi-Spectral Scanner (MSS) and the Thematic Mapper (TM) on the Landsat series of satellites, and the Coastal Zone Colour Scanner (CZCS) which operated between 1978 and 1986 on the experimental Nimbus-7 satellite. The CZCS was the first satellite sensor dedicated to monitoring phytoplankton and sediments in the near-surface waters of the ocean. The bands had narrow bandwidths and high sensitivity tailored to the absorption spectrum of oceanic planktonic pigments, so that chlorophyll concentrations could be determined from the ratios of the radiances in different spectral bands, showing regional and temporal variations in phytoplankton concentration. The CZCS swath-width was about 1600 km and the pixel size 825 m. The Landsat sensors were primarily designed for land applications, but the TM (which has a spatial resolution of 30 m and swath width of 185 km) has proved useful in coastal and bathymetric studies. SPOT is a French satellite with even higher resolution visible sensors (but correspondingly narrower swath) covering similar wavelengths to the Landsat MSS.

The Sea-viewing Wide Field-of-view Sensor (SeaWiFS, scheduled for launch in mid-1997) will provide colour imagery in 8 spectral bands to reveal regions of enhanced biological productivity such as upwelling zones. There have been many unfortunate delays in the launch of this sensor, which will have a swath-width of 2800 km and a resolution of 1.1 km (similar to the AVHRR) and is expected to provide a major boost to coastal oceanic and fisheries-related studies. The Ocean Colour and Temperature Scanner (OCTS) was recently launched on the Japanese Advanced Earth Observing Satellite (ADEOS); it has 8 bands in the visible and near infra-red and 4 in the thermal region of the spectrum, providing coincident visible and thermal imagery with a spatial resolution of about 700 m.

Landsat TM: Bathymetric and habitat mapping

Because visible radiation can penetrate into the water column, the bathymetry and texture of the seabed can be determined under suitable conditions. The shorter wavelengths at the blue-green end of the spectrum can penetrate deeper than the longer (red) wavelengths, so Landsat TM band 1 (0.45 to 0.50 μm) is suited to bathymetric determination while band 2 (0.50 to 0.59 μm) can provide information on the characteristics of the water column. Light reflected from the seabed passes through the water column (where some absorption and scattering by phytoplankton and sediment particles occurs) and then through the atmosphere (with further absorption and scattering) before reaching the satellite sensor. Use of TM imagery for seabed mapping therefore requires the radiances from these component paths to be separated.

Landsat TM imagery has been used to map the seabed in coastal waters off Broome, in Shark Bay, around the Houtman Abrolhos Islands, an area south of Geraldton, in Cockburn Sound and Geographe Bay (Fig 1). The study off Broome examined the relationship between reflectance and depth as well as the spectral reflectance characteristics of pearl oyster habitat (Hick & Scoones 1990). Comparison of data from TM band 1 with hydrographic charts showed that the radiance in this band is highly correlated with bottom depth down to depths approaching 30 m provided the seabed is reasonably uniform, the water clear and the sun high in the sky to provide good illumination conditions. Classification of the substrate in the imagery as reef, sand and seaweed agreed well with visual observations by divers. Plate 5 shows the bathymetric features off Broome, the visible bottom structures being ancient coastlines and wave-cut platforms in water depths exceeding 30 m.

The problem of separating in-water and seabed reflectances has been addressed by Bierwirth *et al.* (1993) using Landsat TM bands 1, 2 and 3 to "unmix" these components in part of Shark Bay (Fig 1), thus providing information on the colour and structure of the seabed as well as estimating the water depth. By assuming a model of the attenuation of radiant flux with depth and the spatial uniformity of suspended materials in the water column, and then applying a constraint to the substrate reflectances for each pixel, both the water depth and bottom type (seagrass meadows, microbial mats and sand) could be determined from the multispectral data.

The distribution of marine habitats at the Houtman Abrolhos Islands has been examined using Landsat TM (bands 1 to 3) and SPOT imagery (Anon 1993, 1994). A number of habitat categories (including sand shallows, coral, seagrass beds and plant-dominated reefs) with different spectral properties were identified from the imagery, aided by aerial photography and diving surveys. Although interpretation of the imagery was ambiguous in waters deeper than 10 to 15 m, it was concluded that the TM and SPOT imagery was useful in providing broad habitat distributions and some new features of the seabed were revealed.

Landsat TM data were also used by Catalano *et al.* (1991) in a study of environmental information for the management of coastal developments (specifically the tourism and fishing industries) along the west coast between

Guilderton and Dongara, south of Geraldton (Fig 1). Mapping of coastal bathymetry to depths of about 10 m, and bottom habitat type was undertaken using Landsat TM bands 1 to 3. While some difficulties were encountered in distinguishing seagrass beds from deeper water and reef systems, and attempts to derive the coastal water circulation were unsuccessful, it was concluded that the use of remotely sensed data showed great potential. However, existing data and/or fieldwork are required to validate interpretation of the satellite information.

Following an earlier study by Gee & Forster (1984) in the moderately turbid waters of Cockburn Sound just south of Perth (Fig 1), Corner & Lodwick (1992) made use of residual modelling to enhance the accuracy of TM depth estimates in waters covering a depth range of 0.3 to 22 m. They found that, under some conditions, the depth estimates could be improved using a calibrated regression relationship between the TM estimates and the surveyed depths (from a chart). Similarly, seabed features in Geographe Bay (Fig 1) could be identified in TM band 1 images at depths down to 45 m under good conditions (Hick *et al.* 1994) using *in situ* radiometric measurements to quantify the effects of suspended sediments and chlorophyll in the water column. The decline in the density of seagrass meadows with increasing depth was evident, as were areas of bare sand where storm events had completely eroded the seagrass.

A wide-ranging description of underwater features (seagrass meadows, reefs, bare sand and deltaic areas) in Western Australia is being undertaken to prepare a national atlas to aid in coastal management (H Kirkman, personal communication). Landsat TM band 1 imagery is being used to prepare maps at a scale of 1:100,000, supported by ground truth observations to confirm features identified in the imagery.

Landsat TM: Island wakes

Small-scale dispersion of coral spawn from reefs is assisted by turbulent wakes and eddies shed from the islands or reefs. Landsat TM imagery has been used to study these wakes behind islands and headlands in Admiralty Gulf, Northwestern Australia, where suspended sediment is visible as a tracer (Pattiaratchi 1994). The structure and behaviour of the wakes depends on an "island wake parameter" involving the size of the island, the regional current speed, the water depth and the vertical eddy viscosity coefficient. Analysis of island wakes and headland eddies identified from satellite data has shown good agreement between the observed wakes and those predicted using the island wake parameter. Plate 6 shows a headland eddy shed from Cape Voltaire in Admiralty Gulf observed in a Landsat TM image; the tidal range in this area is up to 6 m at spring tides, which results in maximum surface currents of 1.5 m s^{-1} and recirculating eddies with dimensions consistent with the theory.

Landsat TM: Water quality

Routine monitoring of water quality parameters such as chlorophyll, suspended sediment, light attenuation, *etc.* in coastal waters may be undertaken using Landsat TM data, and techniques to undertake such studies have been developed for Western Australian estuaries and coastal waters by Lavery *et al.* (1993) and Pattiaratchi *et al.*

(1992). Estimates of the surface chlorophyll concentration and Secchi disk depth (a measure of water clarity) were obtained using the satellite-received radiance corrected for atmospheric effects. The algorithms were developed using water quality data collected at the time of the satellite overpass. The study sites selected were the Peel-Harvey estuarine system (between Perth and Geographe Bay, Fig 1) and Cockburn Sound, two areas where degradation of water quality has been documented over the past few years. The distribution of Secchi disk depths in the Peel-Harvey system derived from a Landsat TM image during a flooding tide clearly showed the frontal structure of the clearer oceanic water (larger Secchi disk depths) and the more turbid estuarine waters (Plate 7).

Landsat MSS: Internal waves

An interesting application of Landsat MSS Band 6 imagery was the identification of internal waves on the Northwest Shelf (Baines 1981). Internal waves exist in the interior of the ocean and tend to form along the interface between layers of fluid of different densities. Associated with these waves are surface bands of convergence and divergence (Robinson 1985) with differing surface roughness visible in satellite imagery. They generally lie parallel to bathymetric features. Baines (1981) interpreted the rough/smooth bands on the sea surface as indicating the presence of tidally-generated internal waves on the thermocline with wavelengths of 300 to 1000 m and propagation speeds of between 0.5 and 1 m s^{-1} .

A more recent (November 1984) Landsat MSS image of the area near Cape Leeuwin has revealed a series of internal waves presumably propagating shorewards from about the position of the continental shelf break, with a wavelength of about 3.5 km (Plate 8).

CZCS: Coastal productivity

The only application of CZCS imagery off Western Australia to date appears to be that of Pattiaratchi *et al.* (1990) who used chlorophyll concentrations derived from the CZCS colour bands and SST from the thermal band to examine the interaction between the Leeuwin Current and the continental shelf waters between Shark Bay and Perth (Fig 1). Chlorophyll concentrations were estimated using standard CZCS algorithms with the removal of atmospheric effects.

Although the absolute chlorophyll concentrations were somewhat uncertain, it was clear that the continental shelf waters contain higher chlorophyll levels than in the Leeuwin Current (Pattiaratchi *et al.*, unpublished observations). Mesoscale meanders sweeping the Leeuwin Current onto the continental shelf were evident in the thermal images, matched by the chlorophyll which acted as a tracer indicating that the current was entraining the productive shelf waters and effectively exporting them offshore (Fig 7). Depending on the degree of entrainment, some offshore meanders/eddies were relatively rich in chlorophyll, with implications for enhanced biological production in these water bodies. SST and chlorophyll transects across the eddies clearly showed the entrainment of the chlorophyll-rich shelf waters into one of the eddies.

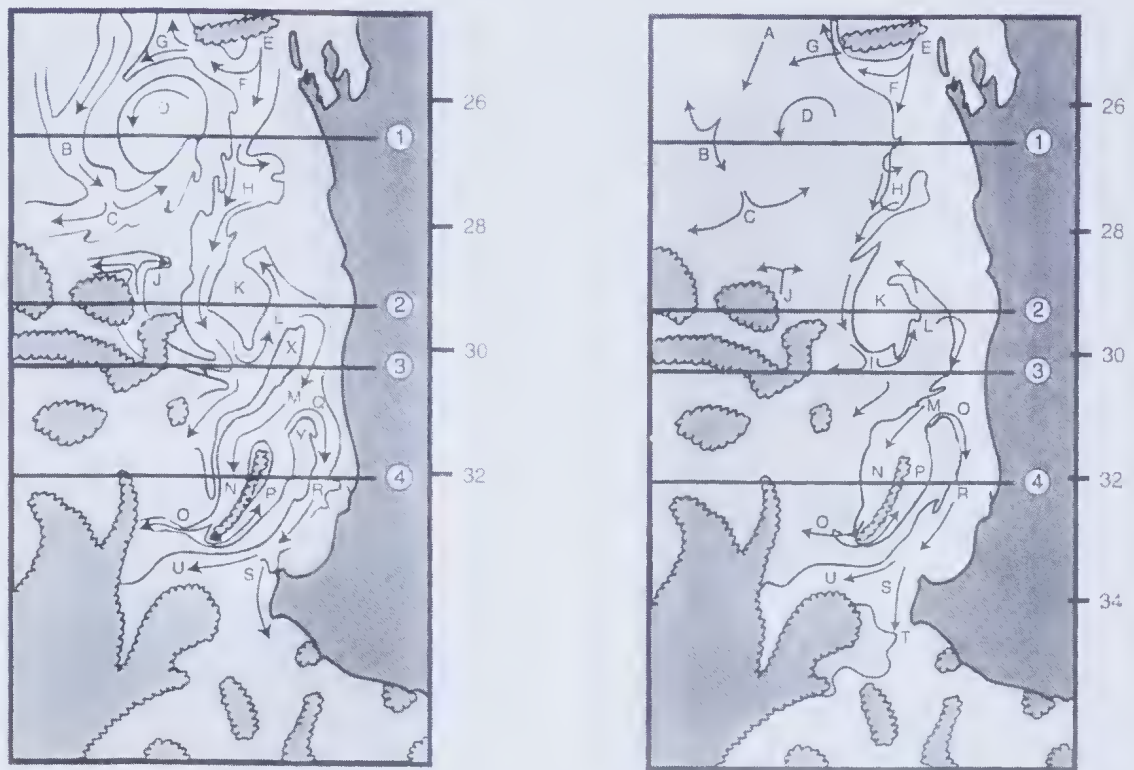


Figure 7. Line sketch interpretations of the Leeuwin Current from (A) CZCS thermal infrared image (band 6) and (B) chlorophyll distribution on 10 May 1981, indicating entrainment of high-chlorophyll shelf waters by the Leeuwin Current. The warm Leeuwin Current is depicted as white in A, as are the relatively high-chlorophyll waters in B. The current arrows have been derived from the SST image A and then transferred to the chlorophyll image B. Features D, K and N-P represent eddies, and the main flow in the Leeuwin Current is along E-H-L-M-N-P-Q-R-S. The densely shaded areas with curly boundaries are clouds. Features A to T and the four transects (solid horizontal lines) are not discussed here.

The future

Understanding the ocean circulation is fundamental to almost all aspects of marine science including biology, fisheries management and research, shipping operations and climate research. There is a growing awareness of the important role played by the circulation in the life histories of many fish and hence in recruitment to commercial fisheries, and the near-realtime tracking of marine pollutants (for example the movement and dispersion of oil spills) by satellite can provide essential and timely information for fisheries managers and pollution authorities to make decisions about appropriate alleviation measures.

Medium resolution thermal imagery (NOAA/AVHRR SST) will continue to provide useful and accessible datasets for monitoring surface features of the large-scale ocean circulation, but is increasingly being supplemented by ocean surface topography. Traditionally, oceanographers have derived the ocean circulation by computing the dynamic height of the sea surface from temperature and salinity profiles, but measurement of sea surface elevation can now be made on a global scale using satellite altimeters such as Topex/Poseidon to yield direct estimates of ocean currents (Fu *et al.* 1994), with the advantage of not being restricted by cloud cover. The distance between the satellite and the sea surface is measured by the time lapse between radar pulses and the return echoes of a narrow beam transmitted vertically downward from the altimeter to the sea surface. The vertical resolution of

altimetric measurements has steadily improved from about 1 m (Skylab) to about 5 cm (Topex; Fu *et al.* 1994) subject to corrections for uncertainties in the geoid, orbit error, atmospheric and ionospheric effects, errors related to sea state, and tides. Acquisition of global sea level data will also allow monitoring of sealevel variability as a result of climate change. Complementing thermal satellite imagery with ADCP-measured currents has confirmed that, at least in subtropical regions with strong boundary currents, surface temperatures generally indicate near-surface current patterns (Cresswell & Peterson 1993).

Most of our present knowledge of global wind and wave conditions has been derived from shipping observations. Satellites can provide wind and wave data on a regular basis over large areas, including remote and inhospitable ocean regions, by recording the roughness of the ocean surface with instruments such as the altimeter, synthetic aperture radar (SAR) and scatterometer (Stewart 1985). The first satellite to carry all these instruments was the short-lived SeaSat (which operated for only about 3 months in 1978), and they are now on the currently-operational European ERS satellites. Satellite-derived wind and wave estimates from the present generation of satellite instruments are comparable with those using *in situ* measurements and are available for coastal wave climatologies and offshore maritime activities such as oil production, shipping and coastal engineering. Routine monitoring of sea state and winds off Western Australia from satellites is very likely in the near future.

Following the important results derived from CZCS colour imagery, the availability of ocean colour data from SeaWiFS and OCTS will greatly improve our understanding of regions where enhanced biological productivity has implications for commercial fisheries operations. High resolution ocean colour imagery will also play an increasingly valuable role in monitoring variations in seabed topography, habitat type (in appropriately shallow waters), coastal pollution and natural tracers such as river plumes.

There will be an ongoing need, however, for validation of remotely sensed data using conventional (surface-based) measurements, a typical example being the need for *in situ* measurements from surface vessels, buoys, etc. to validate satellite-derived surface ocean temperatures. This is particularly true in tropical areas of high atmospheric water vapour loading, where the accuracy of remotely-sensed SSTs is often poor and SST imagery may not be a reliable indicator of either absolute temperatures or circulation patterns.

The advent of new satellites and sensors will provide increased opportunities for use of complementary sensors in different regions of the electromagnetic spectrum, for example the study of surface circulation patterns using both thermal infrared imagery (to show thermal fronts), altimeter data to derive current speeds and ocean colour imagery to track the movement of tracers such as sediments or plankton patches. Because of the vast expanse of ocean recently proclaimed as Australia's Exclusive Economic Zone (EEZ), satellite remote sensing provides the only feasible means of monitoring both physical and biological processes in our surface waters on a regular basis. Conventional oceanographic measurements are still necessary, however, for providing the full 3-dimensional description of the oceans, so satellite remote sensing must be recognised as only another tool available to the marine scientist.

Acknowledgements. This paper has been partly based on information provided by M Grundlingh (CSIR South Africa) as well as by colleagues too numerous to mention individually. Satellite pictures were processed by A Way and C Bowron (CSIRO Division of Oceanography) from imagery supplied by the Western Australian Satellite Technology and Applications Consortium (WASTAC). Landsat TM images have been kindly supplied by P Hick (CSIRO), A Wyllie and R Shaw (WA Department of Land Administration). K Nardi (Abrolhos Islands Consultative Council) and J Stoddart (Marine Science Associates) gave permission to use reports prepared for the Mid-West Development Commission. C Burton undertook the analysis of SST transects off Shark Bay.

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Applications of satellite remote sensing for mapping and monitoring land surface processes in Western Australia

R C G Smith

Remote Sensing Services, Department of Land Administration, Leeuwin Centre, 65 Brockway Road, Floreat WA 6014: richard_smith.dola@notes.dola.wa.gov.au

Manuscript received February 1997

Abstract

Visible and near infrared multi-spectral imagery of the earth from a civilian polar orbiting sun synchronous satellite first became available in 1971 and was first processed in Western Australia in 1974 for research into the broad area mapping of land cover types and geological structures. As other regions of the electromagnetic spectrum have become available on later satellites, applications have expanded. By the 1990s, repeat observations by similar sensors over many years were being used successfully to monitor changes in land surface conditions over large areas. The integrated, synoptic and temporal views of the changing earth is providing scientists with more complete information into land surface changes and associated processes. Regular monitoring by satellite is enabling future outcomes to be forecast and the community to be better involved in solutions. This is illustrated by increased community support for the management of bush fires in the Kimberley region following the introduction of routine satellite monitoring. Future opportunities for expanding such applications are discussed.

Introduction

Western Australia has a sparse population of only 1.7 million, managing a vast area of 253 million ha bounded by over 12,000 km of coastline. As a result there is an increasing use of satellite remote sensing to map, monitor, manage and explore the natural resources of Western Australia. Satellite observations complement aerial photography, where large area coverage is needed, natural features change rapidly or geographic information exists beyond the visible and near infrared parts of the electromagnetic spectrum.

Satellite usage is expanding with the number of hard copy high resolution satellite images produced by the Remote Sensing Services Branch, Department of Land Administration (RSS, DOLA) increasing from about 200

to 700 per year from 1984 to 1995 (Fig 1). The demand of the mineral exploration industry has probably caused a similar expansion in the private sector.

Expanding demand for weather forecasting and for broad scale surveillance to monitor bush fires, drought and sea surface temperatures has contributed to significant growth in the reception and archiving of coarse resolution NOAA satellite data in Western Australia (Fig 2).

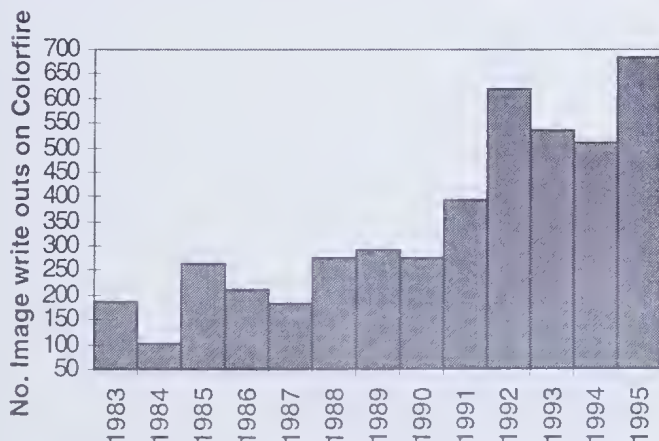


Figure 1. Number of high resolution satellite images produced as high quality photographic prints by Remote Sensing Services, DOLA.

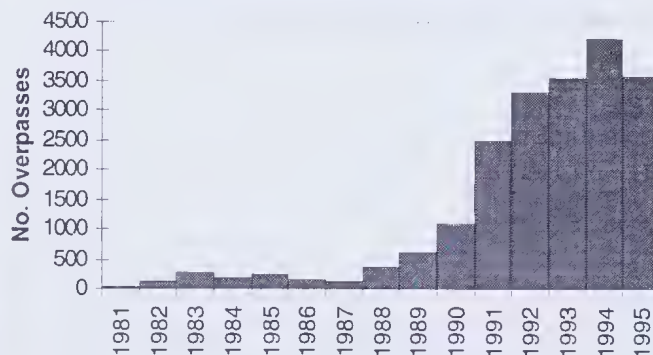


Figure 2. Number of overpasses of the NOAA satellite received and archived in Western Australia.

To outline how these satellite observations of the earth are impacting the quality of life in Western Australia, a general introduction to the principles of remote sensing is given, followed by a brief review of the application of these principles to monitoring and managing land surface processes. Complementary papers cover the applications of satellite remote sensing to oceanography (Pearce & Pattiaratchi 1997) and a bibliography of all publications on satellite remote sensing (research and development) conducted in Western Australia (Smith & Pearce 1997). Some basic texts on remote sensing are Richards (1986),

Lillesand & Kiefer (1987), Legg (1992), Buitens & Clever (1993) and D'Souza *et al.* (1993).

Satellite remote sensing

The ability of people standing on land to observe the earth's surface is extremely confined by space and time, the oblique view angle, and the very narrow portion of the electromagnetic spectrum observed by the human eye. Earth observing satellites extend the human powers of observations by;

- continuous acquisition of data from the nadir view;
- regular revisit capabilities giving regular updates;
- broad regional and global coverage;
- wide coverage of the electromagnetic spectrum in the visible, infra-red, thermal and microwave bands;
- a range of spatial resolutions (from 100 km to 10 metres);
- ability to manipulate and enhance digital data;
- ability to combine satellite digital data with other digital data;
- cost effective coverage of regional, continental and global areas;
- map-accurate data;
- possibility of stereo viewing and digital elevation extraction; and
- large archive of historical data for monitoring changes.

Earth observations using satellites are limited by their fixed revisit times, the complexity of acquiring and processing the data and for the optical wavelengths by cloud cover.

The electromagnetic spectrum

Remote sensing measurements of the earth's surface are non-contact and non-invasive. They are based on measuring the interaction of the electromagnetic spectrum with the earth's surface. Passive remote sensing systems are the most common, where energy from the sun reaches the sensor by reflectance or emittance from the earth's surface. In active remote sensing systems the energy is provided by a radar or laser source from the remote sensing platform itself.

The electromagnetic spectrum includes a wide range of energy, from X-rays through visible light to radio waves. Only a portion of the electromagnetic spectrum can be used for satellite remote sensing due to limits set by the physical interaction of the radiation with the surface or the earth's atmosphere. When the wavelength of the radiation diminishes to the same order as the spacing between the molecules in the surface, the radiation is not reflected but is absorbed. In addition, depending on the wavelength, the energy from the surface being sensed is scattered or absorbed by the atmosphere on the way back to the sensor. This restricts remote sensing at the lower end of the visible wavelengths. The upper limit is set by the need to have reasonably detailed images of the earth therefore use of long wavelength radio waves is impractical. Having set the upper and lower limits, the useable electromagnetic spectrum is divided into six main sections by the absorption properties of the atmosphere (Fig 3).

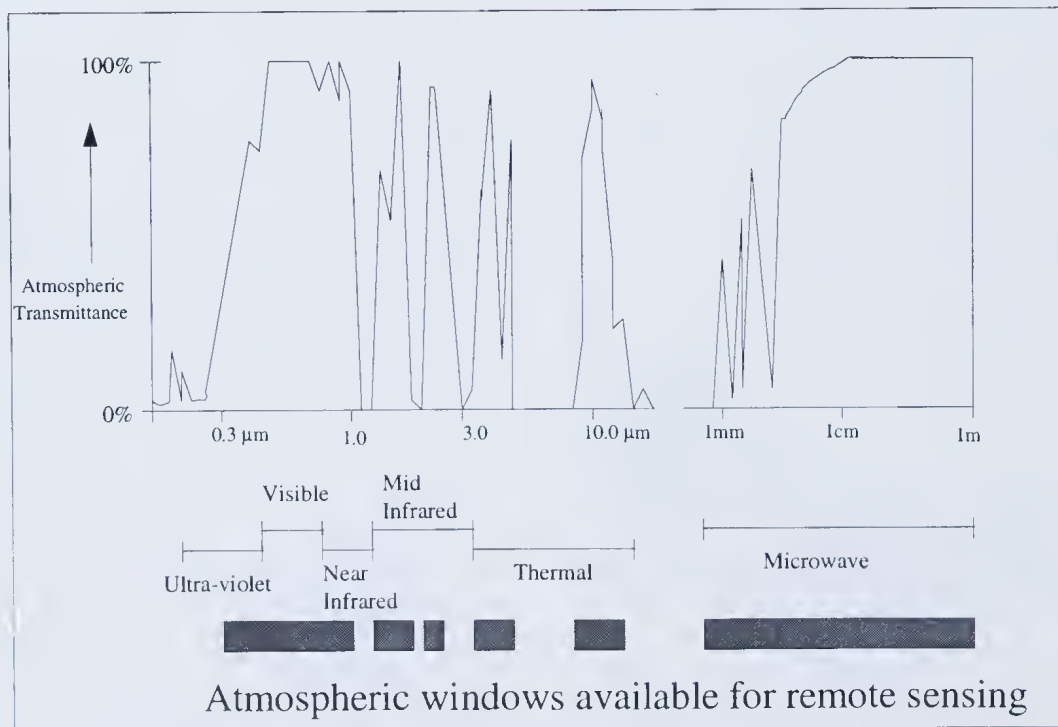


Figure 3. Portions of the electromagnetic spectrum used for remote sensing, showing the main subdivisions and atmospheric windows (modified from Legg 1992).

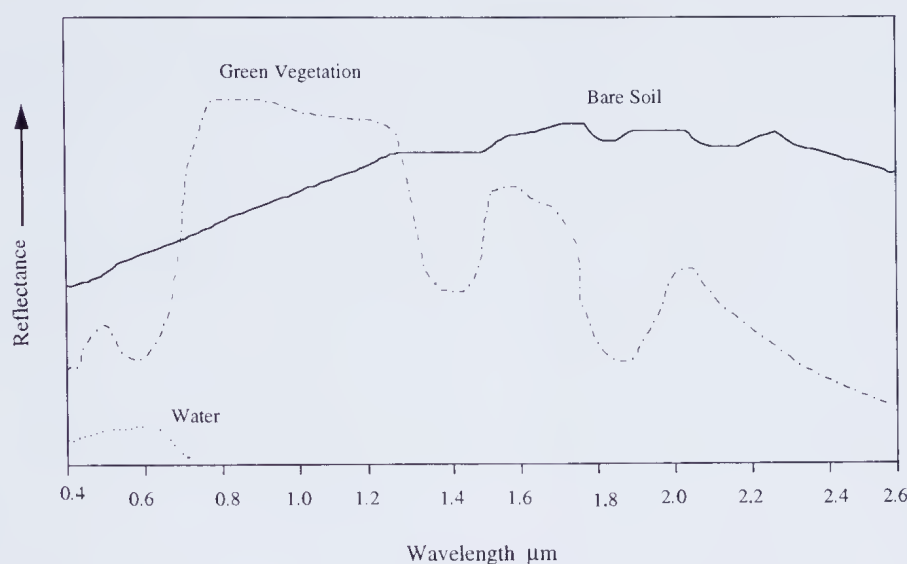


Figure 4. Typical reflectance spectra of dense green vegetation, soil and pure water (Modified from Legg 1992)

Ultraviolet. Atmospheric absorption is very strong in the ultra-violet, limiting satellite applications but applications are feasible using active airborne systems. World Geoscience Corporation in Western Australia operate an Airborne Laser Fluorescence (ALF) instrument at a wavelength of $0.266\ \mu\text{m}$ for oil exploration. The spectra of the fluorescence enables oil films caused by seeps below the sea bed to be identified. Using the same principles, ALF could probably be used for the measurement of algal blooms caused by phytoplankton.

Visible. The largest atmospheric window and the highest amount of reflected solar energy is found in the visible wavelengths, and consequently it is the easiest to measure by satellite sensors in space. The first civilian earth observing satellite sensor, the Landsat Multispectral Scanner, had two of its four bands in the visible region with the third and fourth in the near infrared. Reflectance in the visible wavelength shows little spectral variation for rocks and soil (Fig 4) and is strongly affected by atmospheric scattering which causes a loss of dynamic range which limits contrast. Reflectance in the red part of the visible spectrum is useful for indicating the relative iron content of soils and all visible wavebands are useful for mapping surface geological structures (stratigraphy). Decreased reflectance in the visible part of the spectrum caused by chlorophyll absorption for photosynthesis is used for measurement of vegetation characteristics. Visible wavelengths penetrate water and are scattered back by suspended material and phytoplankton, whereas radiation in the infrared is almost totally absorbed by water (Fig 3). This enables visible wavelengths to be used for remote sensing studies of water quality and for the bathymetry of shallow coastal waters. However the energy levels are low and the dynamic range of sensors optimised for the land surface are often not well suited for remote sensing water characteristics unless the gain setting can be reset.

Near infrared. The near infrared (NIR) portion of the spectrum has similar energy to the visible part and consequently with appropriate filters can be recorded with the same type of sensor. Less absorption and scattering

by the atmosphere occurs in the NIR, resulting in a higher dynamic range and imagery of good contrast.

Natural surfaces are rough, causing shadows. Consequently reflectance is a function of the sun and sensor view angles, giving rise to what is known as the bi-directional reflectance function (BDRF). In addition reflectance from vegetated surfaces with partial canopy cover is affected by the reflectance of the soil background. The NIR in combination with a visible waveband can be used to estimate green vegetation cover (Fig 5). To minimise the effects of season, sun angle and soil background on reflectance when measuring vegetation it is common to use a ratio such as the Simple Ratio (SR) between NIR and red (RED) reflectances;

$$\text{SR} = \text{NIR} / \text{RED}$$

or the Normalised Difference Vegetation Index;

$$\text{NDVI} = (\text{NIR} - \text{RED}) / (\text{NIR} + \text{RED})$$

(Figure 5).

Using the visible and near infrared wavebands, the first civilian remote sensing satellite Landsat 1 was launched in 1971 into a polar sun-synchronous orbit at an altitude of about 900 km (Table 1). Orbiting the earth every 100 minutes at $27,000\ \text{km h}^{-1}$, the MSS sensor scanned a swath width of 185 km and covered the whole earth's surface after 233 orbits over 16 days at a resolution of 80 m. The analog signal was quantised to 6 bits (64 levels) and transferred to earth at a rate of $15\ \text{Mb s}^{-1}$. The spatial resolution of approximately 1 ha per pixel of Landsat MSS is relatively coarse compared with later satellites (compare Plate 1A with B,C,D).

Mid infrared. Use of the mid infrared wavelengths did not become possible until the launch of the Thematic Mapper (TM) sensor on board Landsat-4 (Table 2) in 1983. This spectral region has two atmospheric windows of high transmittance, one centred at $1.5\ \mu\text{m}$ and the other at $2.2\ \mu\text{m}$ (Fig 3). These wavebands are of importance in geological and vegetation studies. The relatively low level of reflected radiation at MIR wavelengths requires more sophisticated sensors and cooling to achieve high signal to noise. Landsat-TM also provided 30 m resolution

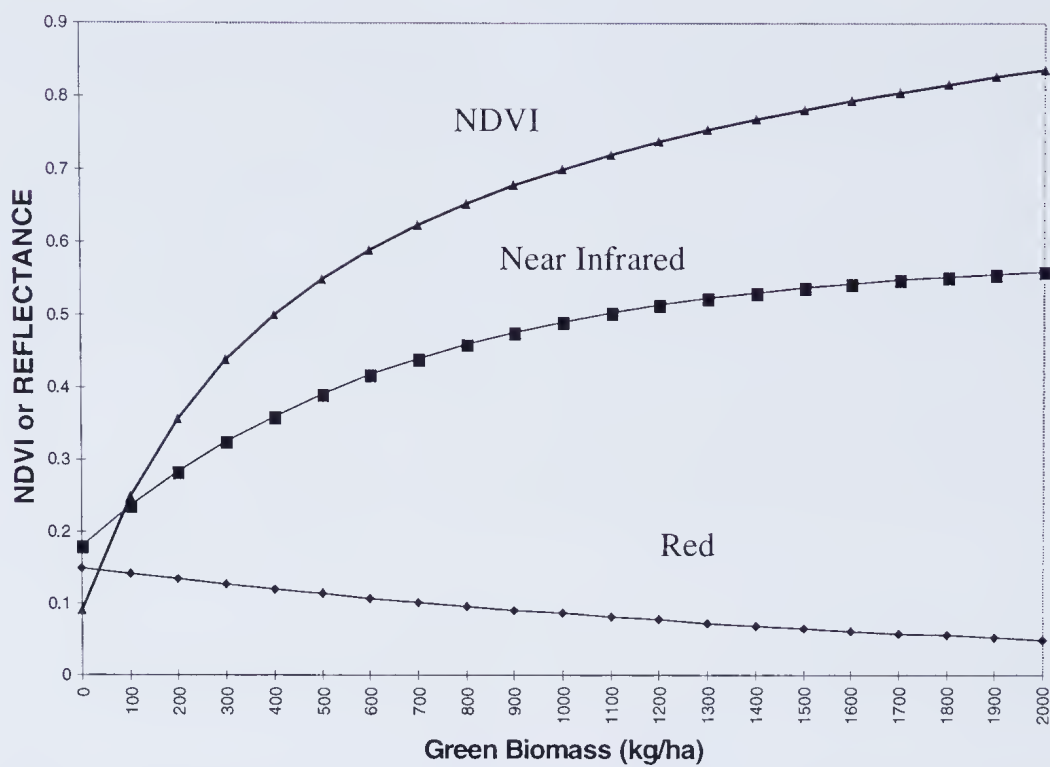


Figure 5. Hypothetical relationship between RED and NIR reflectances and the NDVI as a function of green biomass.

Table 1
Characteristics of Landsat Multi-Spectral Scanner (MSS).

Band	Wavelength (μm)	Description	Applications
1	0.5-0.6	Visible - green	Water studies
2	0.6-0.7	Visible - red	NDVI, water, soils
3	0.7-0.8	Red to Near Infrared	NDVI, topographic mapping
4	0.8-1.10	Near Infrared	NDVI, topographic mapping

Table 2
Characteristics of Landsat-TM.

Band	Wavelength (μm)	Waveband	Applications
1	0.45-0.52	Visible Blue	Water and urban studies
2	0.52-0.60	Visible Green	Water and urban studies
3	0.63-0.69	Visible Red	Water and vegetation studies
4	0.76-0.90	Near Infrared	Vegetation and topography
5	1.55-1.75	Mid Infrared	Vegetation, especially forestry
6	10.4-12.5	Thermal Infrared	Water, land surface temperatures and evapotranspiration
7	2.08-2.35	Mid Infrared	Soils and minerals

Table 3
Characteristics of the sensors on the SPOT satellite.

	Multispectral Mode (XS)	Panchromatic Mode (PAN)
Spectral Bands (μm)	0.50-0.59 0.61-0.68 0.79-0.89	0.51-0.73
Pixel size	20 m	10 m
Swath width	60 km	60 km
Repeat cycle	21 days	21 days
Steerable ± 27°	1-4 days revisit	1-4 days revisit

for all bands with 120m for the thermal infrared. This improvement in resolution can be seen by comparing Plate 1B with 1A from Landat-MSS. The Thematic Mapper was designed for mapping land cover themes and to improve precision the analogue signal was quantised to 8 bits (256 levels). The increased amount of data is transmitted to the earth at a rate of 85 Mb s⁻¹, which resulted in expensive X band reception facilities being provided by the Commonwealth Government at Alice Springs in 1987 for local reception. Landsat-TM has been the main satellite sensor used in high resolution remote sensing in Western Australia since 1987. Band 7 is in a region where the phyllosilicates such as clay minerals show absorption peaks. Therefore it was included at the insistence of geologists and has proved of value in lithological mapping and in the discrimination of clay-rich alteration zones. Band 5 is sensitive to the surface water content, therefore it is responsive to the amount and condition of vegetation. The broad width of these two wavebands restricts the amount of mineralogical information that can be derived. A multispectral capability in the MIR region is required to extract this information.

The high resolution Landsat-TM data was later exceeded by the 20 and 10 m resolutions of the French SPOT satellite launched in 1986 (Table 3; Plate 1C,D). However, the higher cost and absence of routine coverage and lack of a mid infrared band has limited the application of SPOT multi-spectral data in Western Australia. The panchromatic data is often merged with Landsat-TM to improve the quality of the imagery for mapping surface features. SPOT with its steerable sensor enables stereo pairs to be acquired for digital elevation extraction. SPOT-4, due to be launched in 1997 (CEOS 1995), will have a mid-infrared band from 1.5-1.7 µm and a wide field of view sensor, named the VEGETATION sensor with a swath width of 2,200 km and resolution of 1 km. An image based on a general enhancement of Landsat-TM using bands 7,4 and 1 is commonly produced to assist geological mapping by the Geological Survey of Western Australia. An example of this enhancement from inland Australia is given in Plate 2.

Thermal infrared. This region includes two distinct atmospheric windows (Fig 3), separated by a strong atmospheric absorption zone caused by water vapour. Remote sensing in this region is similar to the mid infrared with low energy levels associated with emitted radiation. Special detectors, cooling and optics are required to get a high signal to noise ratio. Development of civilian space-borne thermal infrared sensors was driven by meteorologists who required measurements of sea surface and cloud top

temperatures. The first polar orbiting satellite to provide thermal infrared sensors was the NOAA-Advanced Very High Resolution Radiometer (Table 4). It was launched in 1979 following a successful prototype first launched in 1974.

Designed for meteorological applications, NOAA-AVHRR has a wide field of view sensor covering a swath width of 2,800 km with a resolution of 1.1 km at nadir and transmitting at 665 kb s⁻¹. Bands 1 and 2 are used for detection of clouds, vegetation measurement and detecting firescars. Band 3 is used for detecting fires, as at this wavelength the sensor does not saturate at high temperatures and has the sensitivity to detect gas flares from the oil platforms on the NW shelf. Bands 4 and 5 provide cloud, land and sea surface temperature measurements. Based on differential absorption by the atmosphere, use of the two bands (4 and 5) can be used to empirically correct for atmospheric effects. The NOAA-AVHRR data has high radiometric resolution with 10 bit quantisation (1024 levels) and on-board black body calibration of the thermal sensors. Lack of on-board calibration of bands 1 and 2 has made accurate long term measures of vegetation difficult due to changes in sensor response over time. These changes occur when new NOAA satellites are launched, sensors age and overpass times drift later causing decreasing sun illumination angles.

NOAA-AVHRR is a American meteorological sensor whose data is free as part of a World Meteorological Agreement. Compared with Landsat-TM, NOAA-AVHRR provides high temporal resolution (daily *vs* 16 day coverage) but low spatial resolution (1 km *vs* 30 m), which keeps data handling manageable and makes economic local L-band reception (*ca.* \$50,000) compared with X-band reception (*ca.* \$2 million). This affordable capital cost has enabled operational use of NOAA-AVHRR to monitor seasonal vegetation growth, bush fire risk, fires, fire scar mapping and sea surface temperatures to be developed by RSS, DOLA. Operational monitoring of green vegetation cover is made using the NDVI (Plate 3) and achieved by combining successive NOAA overpasses over 14-16 day periods to produce cloud free images at the middle and end of each month.

The wavebands in the thermal infrared region contain significant geological information. Temperature differences between day and night often reveal buried geological features based on differences in specific heat. Differences in thermal emissivity are of value in lithological discrimination, but requires a multispectral capability that will be available on a proposed Japanese/American satellite.

Table 4
Characteristics and applications of the NOAA-AVHRR satellite sensor

Band	Wavelength (µm)	Waveband	Applications
1	0.58-0.68	visible	Surface features, cloud, vegetation, albedo
2	0.73-1.10	near infrared	Water, vegetation, firescars, albedo
3	3.55-3.93	thermal	Fires and volcanoes
4	10.5-11.3	thermal	Sea, land, cloud temperature and evaporation
5	11.5-12.5	thermal	Sea, land, cloud temperature and evaporation
Swath	2,800 km	Scan angle	± 55.4°, Resolution at nadir 1.1 km
Revisit	12 hours	Repeat cycle	9.2 days

Other wide field of view sensors (WiFs). The coarse resolution of the NOAA-AVHRR satellite restricts its use in agriculture as individual agricultural fields on the ground cannot be resolved. However WiFS sensors on the Russian RESURS-01 and Indian IRS-1C satellites (CEOS 1995) provide data in the visible and NIR wavebands at 170 m resolution that could be ideal for agricultural monitoring.

In addition to the above satellites which are polar orbiting and sun synchronous, Western Australia is observed by the Japanese Geosynchronous Meteorological Satellite (GMS-5) which is situated in a geostationary orbit at 140° E, 36,000 km above the equator. The 36,000 km distance compared with the 700 to 900 km of the polar orbiting satellites is required to maintain the satellite in orbit while orbiting at the same rate as the earth. The GMS satellite has a Visible (0.5-0.75 μm) and Infrared (10.5-12.5 μm) Spin Scan Radiometer (VISSR) which scans the earth from horizon to horizon every hour. The data is transmitted to Japan for processing before transmission to Melbourne, Australia for meteorological forecasting.

Microwave. The microwave portion of the spectrum is divided into a series of bands known as C band (6 cm), S band (13 cm), L band (25 cm) and P band (68 cm). Passive remote sensing of microwave emissions from the earth's surface by the Special Sensor Microwave/Imager (SSM/I) on the DMSP (Defence Military Satellite Program) is used for ice monitoring and precipitation measurement at spatial resolutions of 10-100 km. Active remote sensing systems based on synthetic aperture radar (SAR) are used to get higher resolutions of 10-30 m. The shorter microwave wavelengths are more strongly absorbed by natural material and the longer wavelengths penetrate further into the soil and overburden. The amount of energy scattered back to the sensor depends on the dielectric constant of the surface and its surface roughness. A major application of SAR is in tropical areas where dense cloud can prevent observations by optical sensors. In these areas the main applications appear to be mapping geological structures and changes in land cover such as deforestation. Several satellites have been launched with SAR sensors, the main ones being the Japanese Earth Resources Satellite (JERS-1) with L band launched in 1994, the European Earth Resources Satellite (ERS-1) with C band launched in 1991 and the commercial Canadian RADARSAT-1 with C band, HH polarisation and variable look angle launched in 1995. Projected future uses for SAR data are monitoring of floods, ice fields and oil spillage dispersed on the water surface. To date no significant applications in Western Australia have emerged for SAR data.

Other specialist radar sensors that might find oceanographic application in Western Australia are the altimeters and scatterometers. The altimeters on ERS-1 and TOPEX/POSEIDON measure deviations of the sea's surface height from the theoretical geoid to give estimation of the gravity field below the ocean and ocean currents on the surface. The wind scatterometer on ERS-1 records the change in radar backscatter of the sea caused by the wind close to the surface. Wind direction is derived from the orientation of the backscatter relative to the orientation of the pulse of microwave radiation transmitted by the scatterometer. These data are becoming available operationally and are being used in weather forecasting.

NASA is using a wind scatterometer on Japan's Advanced Earth Observing Satellite (ADEOS) to send wind data every 2 hours to US weather forecasters (Gibbs 1996). Scatterometer data can also be used to measure vegetation types (Long & Hardin 1994).

Developments using airborne sensors

The development and application of satellite sensors has been assisted by experience gained with airborne multispectral scanners such as the GEOSCAN which was built locally in Western Australia and widely used in mineral exploration and environmental monitoring. At a lower cost, a Digital Multi-Spectral Video (DMSV) which uses four CCD video cameras with filters giving wavebands typical of Landsat MSS for vegetation and water measurements has been developed locally. Demonstrating the potential value of SAR data from satellite, NASA has flown the Airborne Synthetic Airborne Radar (AIRSAR) instrument in Western Australia for experimental purposes. This instrument has P, L and C-band with four different polarisations (HH, HV, VH and VV) and a duplicate set of sensors with L and C-bands at VV polarisation (TOPSAR) for interferometry measurement of elevation. This multiple range of frequencies and polarisations will become available on later satellite SAR sensors.

Use of satellite data for surface geological mapping complements a range of ground penetrating geophysical airborne instruments that are flown to map various below ground geological features. These instruments measure magnetics, conductivity (electro-magnetics) and gamma ray emissions (radiometrics). To aid geologic interpretation of the distribution of weathering products in the landscape, it is common to merge airborne radiometric and Landsat-TM satellite data.

Sensors of the future

The application of satellite remote sensing is still young. Over the next 15 years another 80 missions are planned with over 200 sensors proposed (CEOS 1995). Capturing the benefits from these sensors will be a challenge to researchers and applications scientists. Developments in microelectronics creates new sensors, lower weight satellites, faster communications and more powerful computers to process the data. Spatial resolution will increase from 10 m to <1 m creating digital photogrammetric applications. Hyperspectral data (e.g. 256 spectral bands with 0.08 μm bandwidth in the optical wavelengths) will increase spectral resolution for enhanced applications in mineral detection and environmental monitoring. New radar satellites will have a wider range of microwave frequencies and polarisations. Without loss of spatial resolution, temporal resolution will be increased through the use of constellations of earth observing satellites to enable the monitoring of dynamic changes such as crop growth in agricultural fields and grass growth in rangelands.

Capturing the economic and environmental benefits of these sensors for Western Australia will require a continued growth in local research and development. Timely acquisition for monitoring may require the establishment of a local X-band reception capability.

Development of terrestrial applications of remote sensing

Given these technological opportunities, significant initiatives by Commonwealth and State Government agencies have helped develop applications of satellite remote sensing in Western Australia (Smith & Pearce 1997). The bibliography compiled by Smith & Pearce (1997) indicates that the first recorded publication on terrestrial applications was by Honey *et al.* (1978) using Landsat MSS, for the classification of wetlands on the Swan coastal plain. This classification was based on the spectral differences of wetlands from the surrounding land. The next publication (Houghton 1979) reports the coordination of remote sensing activities which has been an important feature of the successful development of remote sensing in Western Australia where resources for the development of this new technology have been limited. Development of marine applications is covered by Pearce & Pattiaratchi (1997).

Landcover type

The bibliography records that landcover types mapped over the following 16 years using Landsat MSS and TM were mangroves (Honey & Hick 1981), tropical rainforests in the Kimberley (Kay *et al.* 1990), areas of remnant native vegetation in the agricultural area (Campbell & Wallace 1989), forest cover of water catchments (Wyllie & Barile 1990) and areas of gravel suitable for road building (Wyllie *et al.* 1992). The mapping soon extended to geological structures using Landsat data (Smith & Green 1979) and subsequently NOAA-AVHRR (Honey & Tapley 1987; Tapley & Wilson 1986). There are many other significant applications to geology and exploration that are not covered in this review. The significance of this geological use is indicated by the fact that about 60% of all satellite data purchased in Western Australia is used for geological mapping or exploration. The outcomes appear not in scientific publications but as improved geological maps from the Western Australian Geological Survey and the finding of new mineral deposits by the exploration industry.

High resolution satellite imagery is periodically ordered by State agencies such as the Ministry of Planning, Department of Environmental Planning, Ministry of Transport, Department of Agriculture, Department of Conservation and Land Management and the Bush Fires Board for mapping urban development, status of wetlands and new roads, status of National Parks and bush fire assessment.

Land degradation

Degradation has been the subject of a number of studies using classification or visual interpretation to map areas of agriculture affected by wind erosion (Carter & Houghton 1981), salinity (Currey *et al.* 1981; Furby 1994; Wheaton 1992; Wheaton *et al.* 1992) and waterlogging (Wallace & Wheaton 1990; McFarlane *et al.* 1992) and areas of forest affected by dieback *Phytophthora cinnamomi* (Behn & Campbell 1992) and insect damage (Behn *et al.* 1990). The success of the spectral technique for mapping salinity has been recently enhanced by integration of satellite data with information derived from digital elevation data (Caccetta *et al.* 1995a,b; Plate 4). Following the demonstration of the potential, the State

Government plans to adopt this technology to map the extent of salinity and condition of remnant vegetation in the agricultural area to help combat these major environmental problems.

The low albedo of native vegetation compared with agricultural crops (Smith *et al.* 1992) means that spectral information in the visible, near infrared and mid infrared regions is ideally suited for mapping areas of remnant native vegetation in agricultural areas and water catchments (Wallace & Furby 1994). The first comprehensive mapping of changes in the area of native vegetation in the agricultural area from 1991-1991 using Landsat-TM data is currently being attempted. This work is being contracted by the Commonwealth Bureau of Resource Sciences to establish the sources of CO₂ causing the greenhouse effect. Water quality associated with land degradation has been successfully measured using spectral measures of water colour (Pattiaratchi *et al.* 1991, 1992, 1994). Such measures are dependent on relatively smooth water to avoid the sunglint and turbidity caused by rough water. Sequential measures of sea surface water temperatures have been used to estimate currents in the Indian Ocean (McAtee 1992).

Using the Coastal Zone Colour Scanner (CZCS) on the experimental Nimbus-7 satellite, measurement of ocean chlorophyll associated with land degradation has been demonstrated by Pattiaratchi *et al.* (1990). Future use of satellite measures of ocean chlorophyll in Western Australia awaits the anticipated launch of the Sea viewing Wide Field-of-view Sensor (SeaWiFS) in 1997 (Davies *et al.* 1994). More detailed discussions of these applications in the marine environment is contained in Pearce & Pattiaratchi (1997).

Atmosphere

Operational use has been made of satellites in Western Australia to measure atmospheric conditions. The TOVS (Tiros Operational Vertical Sounder), a set of three instruments on the NOAA satellite, is used by the Bureau of Meteorology to measure longwave emittance in a large number of wavebands for a 60 km foot print. From the solution of the radiative transfer equation, the vertical distribution of temperature and moisture is derived for use in operational weather forecasts by the Bureau of Meteorology. Lynch & Marsden (1992) have also derived estimates of aerosol optical depths from NOAA-AVHRR data.

NOAA-AVHRR also offers opportunity to measure cloud top temperatures and cloud climatology associated with changes in vegetation cover. For example, clearing of native vegetation and replacement by annual agricultural species has been observed to cause a decrease in formation of convective clouds (Lyons *et al.* 1993; Lyons *et al.* 1996). Further study of this process is occurring at Murdoch University using NOAA-AVHRR data. In Africa the duration of cloud top temperatures below a certain threshold determined from the European geosynchronous meteorological satellite is used to forecast the spatial distribution of rainfall in areas where rain gauges are sparse.

Land surface processes

Satellite imagery is used periodically by Remote Sensing Services, Department of Land Administration (RSS,

DOLA) to analyse the impact of flooding events on rail, road and pipeline links to assist in assessing the suitability of these engineering structures as they cross the landscape. These images have been enhanced using digital elevation models to create 3D perspectives of the distribution of flood waters. These 3D perspectives are also widely sought after as an aid to geological interpretation (Davison 1992). The possibility of digital elevation extraction using stereo pairs from the SPOT satellite also exists but has not been used in Western Australia, where elevation information from aerial photography is readily available.

Energy fluxes at the land surface over large areas can be studied by using NOAA-AVHRR data to help solve the energy balance equation of the surface. This approach has been used to study the impact of large scale clearing of native vegetation in south western Australia on sensible and latent heat fluxes (Lyons *et al.* 1993, 1996). It was found that the higher albedo following clearing of land for agriculture caused lower sensible heat flux. This lower sensible heat flux causes reduced convection indicating a possible mechanism for the observed 20 to 30 % decline in rainfall that has followed large scale land clearing in south-western Australia.

Monitoring and forecasting land cover changes:

Accurate monitoring is a powerful information tool for increasing public awareness to achieve desired management outcomes. Repeat observations by satellite sensors offer the possibility of monitoring changes in key environmental variables on a routine basis. Areas of bush fires, drought, salinisation, wind erosion, poor agricultural productivity, remnant native vegetation and plantations are examples of changes that can now be routinely monitored. From such changes the processes can be modelled, future outcomes forecast, public support enrolled and better management decisions taken. This forecasting application has been demonstrated by Caccetta *et al.* (1995) for salinity, Smith *et al.* (1995) for wheat yields, and Lyons *et al.* (1996) for the impact of clearing on rainfall.

An example of monitoring and forecasting environmental change is the operational measurement of variations in green vegetation cover at 14 to 16 day intervals across Western Australia using the NDVI from NOAA-AVHRR (Plate 3). Seasonal vegetation growth determines the outcome of later events such as fuel load build up

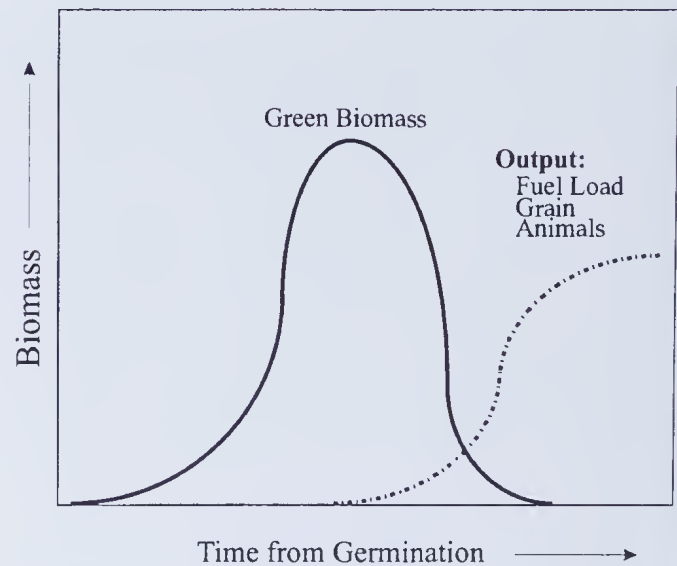


Figure 6. The hypothetical relationship between the seasonal growth of vegetative biomass of annual species and the resultant output of grain, animal products and fuel load.

that sustain fires, drought caused by feed deficit, crop yields and production of grazing animal, which can therefore be forecast (Fig 6).

Monitoring of variations in seasonal vegetation growth of winter-growing Mediterranean annual species in the agricultural area of south-western Australia from NOAA-AVHRR data is shown in Figure 7. Every season, following the winter rains, there is a pronounced period of vegetation growth marked by a rise in the NDVI about May/June rising to a peak in September/ October (Fig 7). There is then a decline as the annual pastures and crops senesce.

The variations in the peak NDVI across the grain belt of Western Australia are closely related to the grain yield of wheat (Fig 8). This close relationship between biomass around anthesis estimated by the NDVI in mid season and final grain yield can be used to forecast wheat yields in December (Fig 8). Similar relationships between paddocks using NDVI calculated from Landsat-TM and SPOT XS data and wheat yields exist and are used to produce yield maps of farmer's fields (Stovold *et al.* 1996).

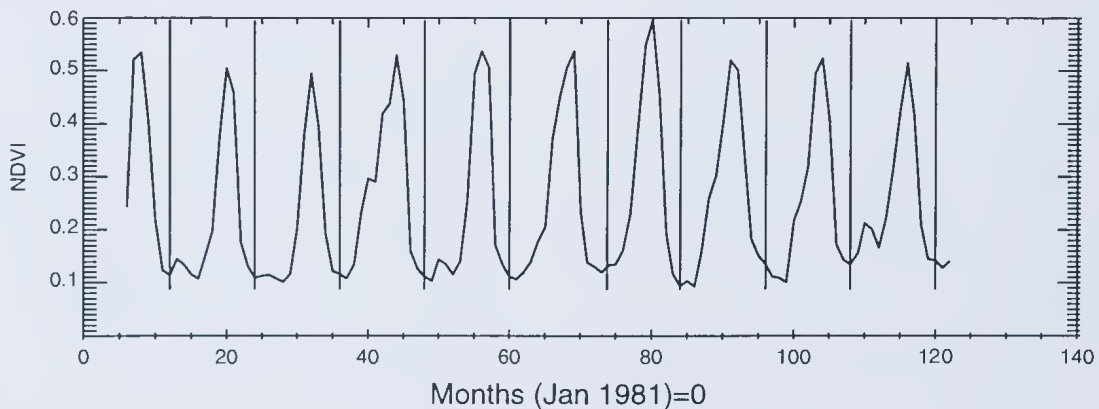


Figure 7. Monthly NDVI time series from NOAA Global Area Coverage data from 1981-91 for a location in the central grainbelt of Western Australia.

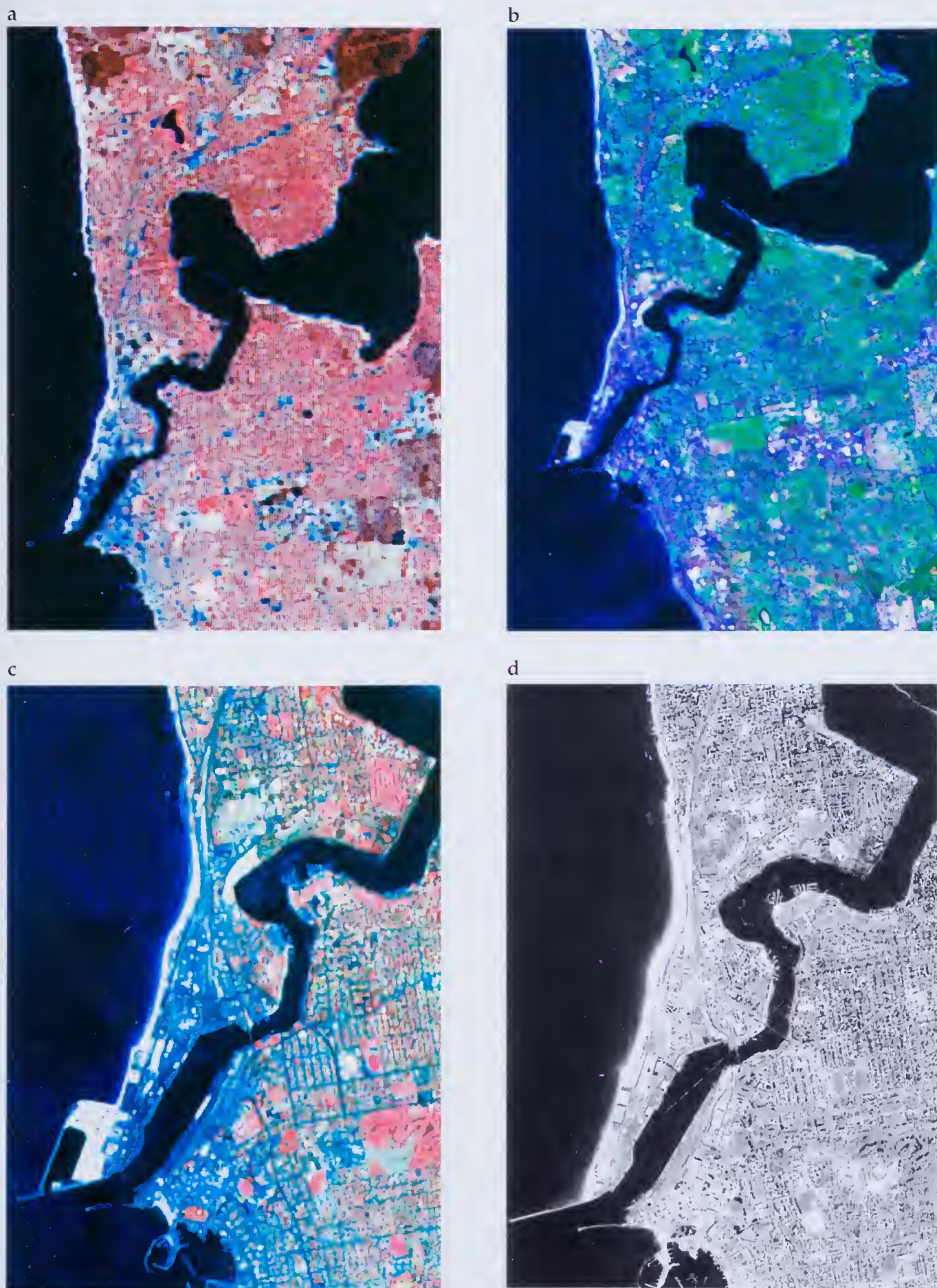


Plate 1A,B,C,D. Comparison of images of the Port of Fremantle and the Swan River, Western Australia to indicate the change in spatial resolution from 1971 to 1986: (a) Landsat MSS (80m) (b) Landsat-TM (30m), (c) SPOT XS (20m) and (d) SPOT PAN (10m).

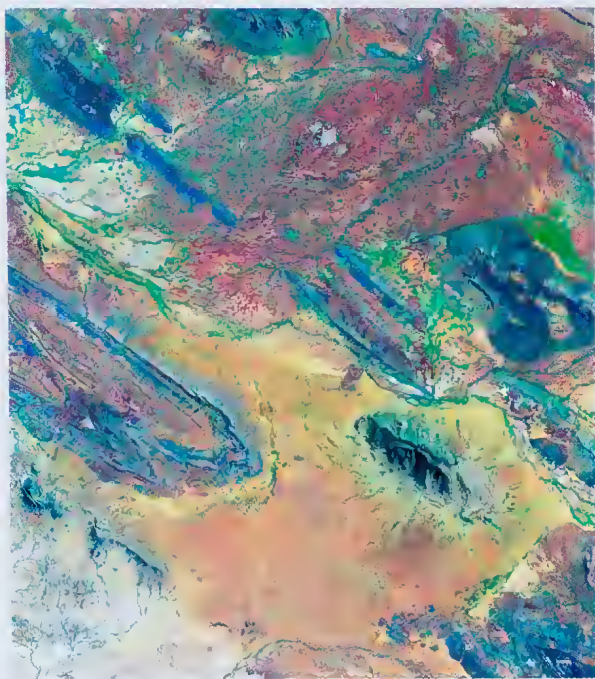


Plate 2. An image map of sheet 2249 of the Australian 1:100,000 topographic series covering Mt Augustus produced from Landsat-TM bands 7,4,1 (Red, Green and Blue) produced for use in geological mapping. Mt Augustus, or Burringurrnah as it is known to the Wadjari Aboriginal people, is about 800 km north of Perth. It is one of the most spectacular solitary peaks in the world. It rises 717 metres above the surrounding plain and is about 8 km long. The dark coloured peak is evident in the lower right hand quarter of the image

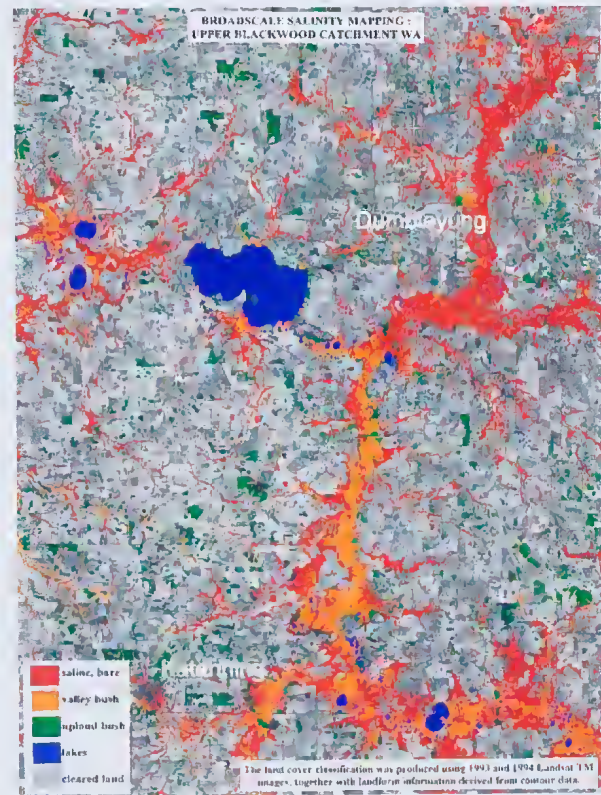


Plate 4. A typical application of Landsat-TM is to map areas of salinisation by classification. This example is an area of the grain belt of Western Australia, 200 km south east of Perth covering an area of about 2,000 km². The technique uses two successive Landsat-TM images during the winter period of crop growth and digital elevation data to classify areas affected by salinity.

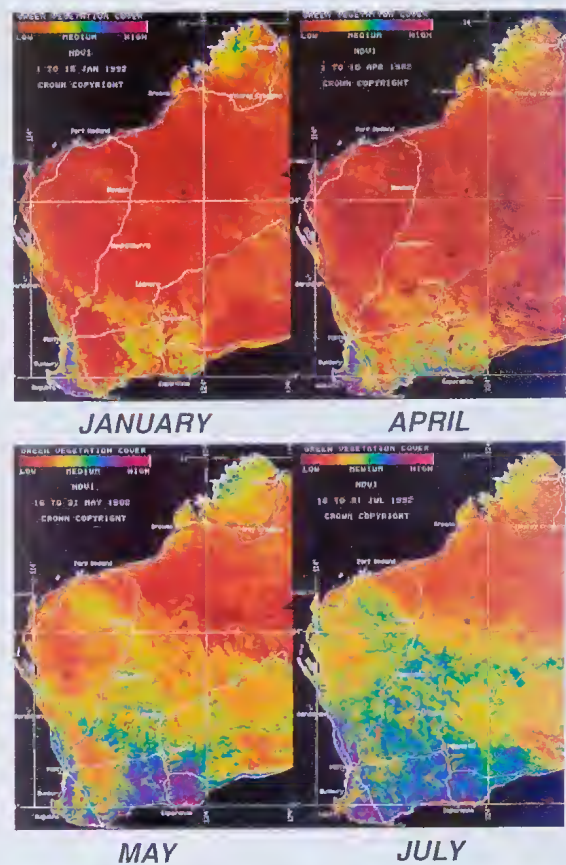


Plate 3. A sequence of images of green vegetation cover of Western Australia based on the NDVI derived from successive overpasses of the NOAA-AVHRR sensor over a 14 to 15 day period using maximum value compositing. The area covered is some 252 million ha.

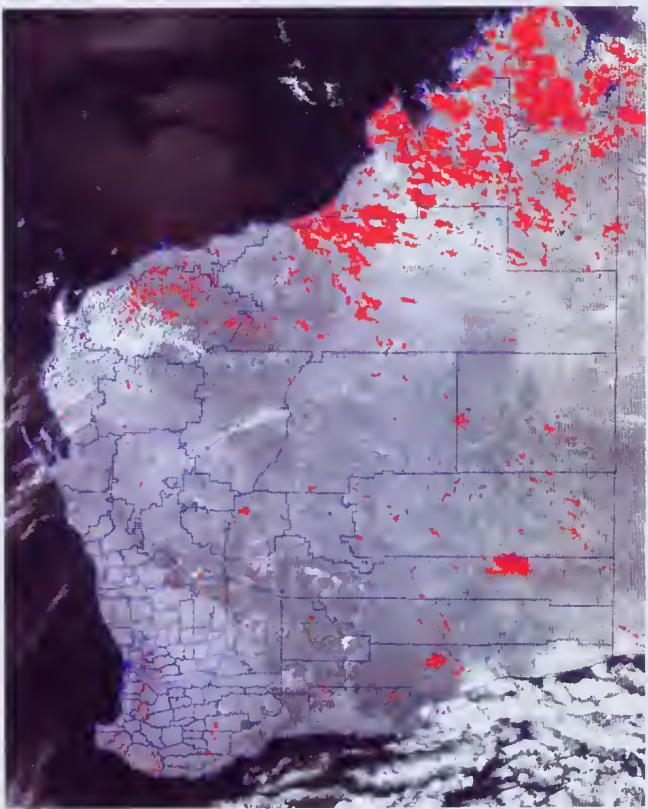


Plate 5. Areas burnt by fires between April 1995 and March 1996 mapped from the NOAA-AVHRR sensor at 10 day intervals.

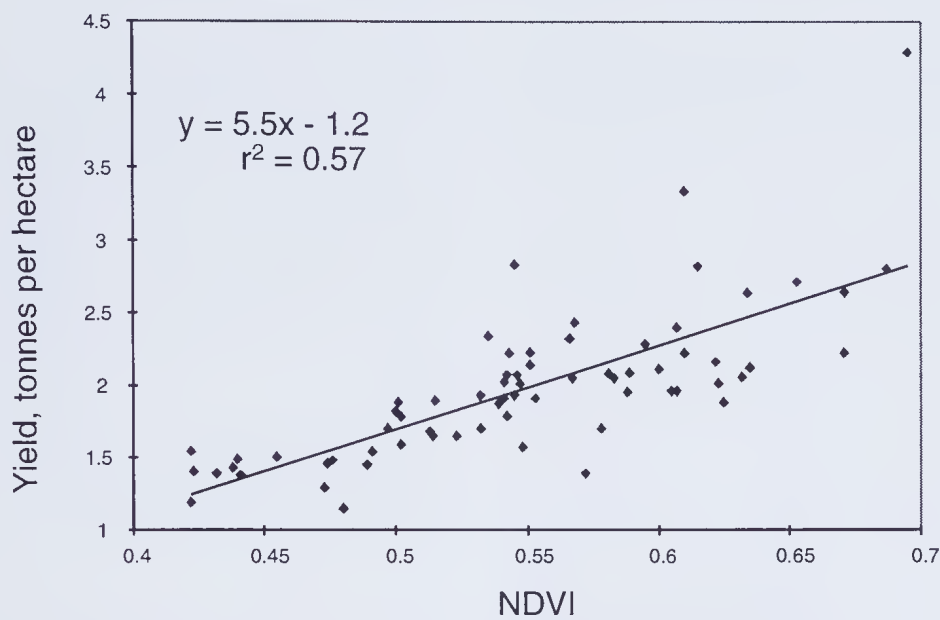


Figure 8. Relationship between the mean NDVI in September 1995 from NOAA-AVHRR data and wheat yield (tonnes ha⁻¹) of 68 local government areas in the Western Australian grain belt (Smith *et al.* 1995).

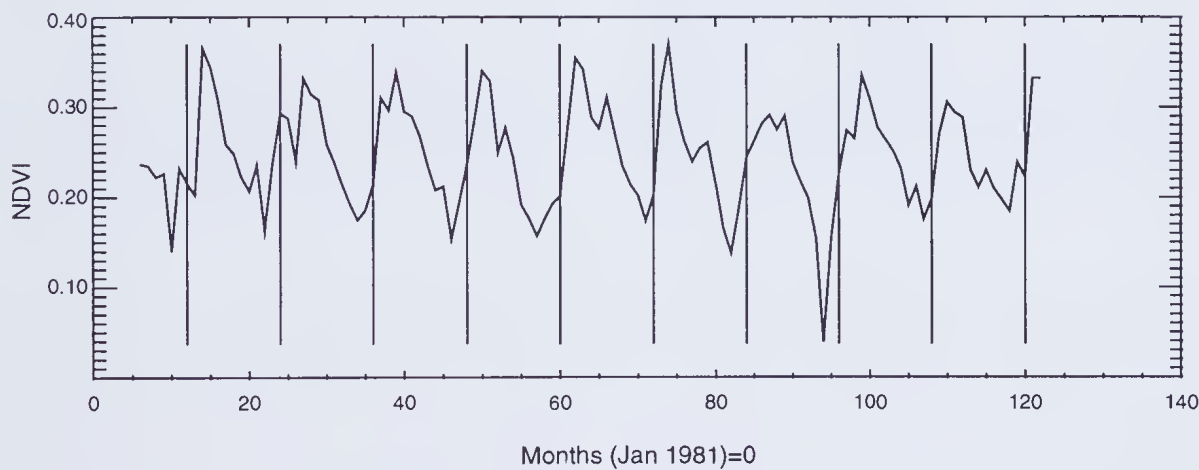


Figure 9. Monthly NDVI time series from NOAA-AVHRR from 1981-91 for the Kimberley area of north-western Australia (note the change in scale from Fig 8).

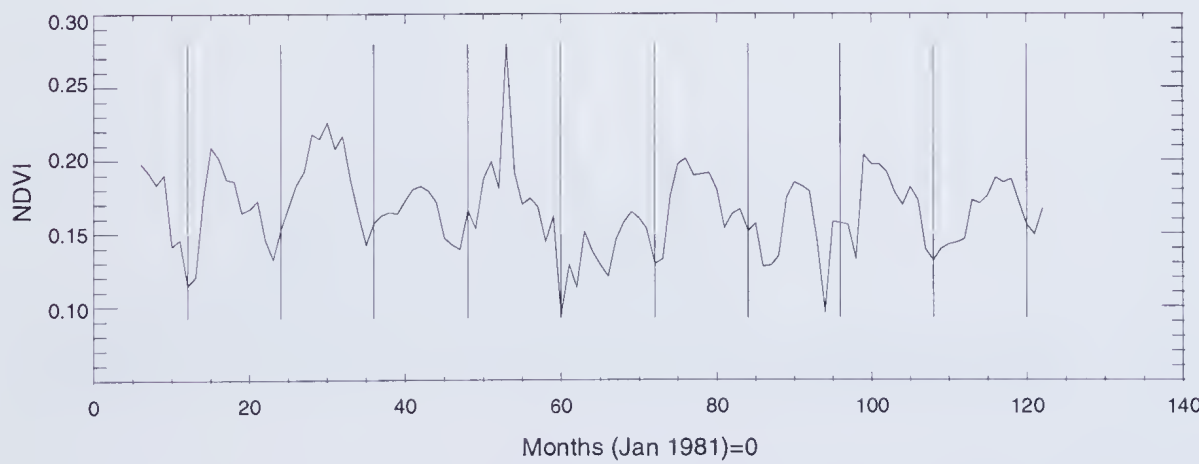


Figure 10. NDVI time series from NOAA-AVHRR GAC data from the central desert area of Western Australia (note the change in scale from Figs 8 and 9).

In north western Australia, which experiences summer monsoonal rains, there is a similar pattern of seasonal vegetation growth with a lower range in NDVI beginning in December and ceasing in about April (Fig 9). The seasonal distribution of this information is used by the Bush Fires Board in Western Australia to monitor the rapid build up in fuel load which provides the basis for extensive bush fires ignited by a variety of natural and human causes. It is also used to plan controlled burning by the Bush Fires Board.

In comparison, the seasonal growth in the inland areas of Western Australia, with lower and more variable rainfall, is much less and more varied (Fig 10). Comparison of current seasonal trends in the NDVI with the long term trend has been used to map areas affected by drought in pastoral areas (Cridland *et al.* 1994).

Near real-time mapping of bush fires for the Bush Fires Board covering the whole of Western Australia has been implemented (Smith *et al.* 1996; Plate 5). The outcome of this fire monitoring in 1995/96 was the detection

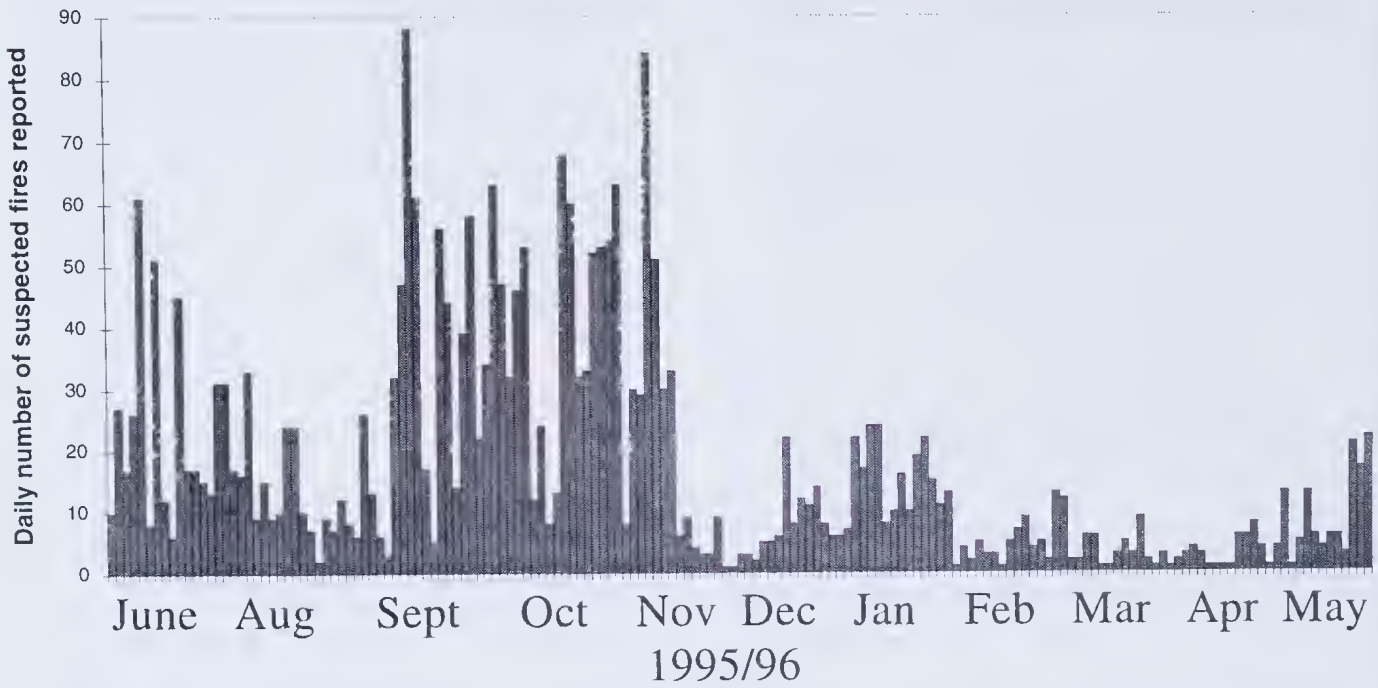


Figure 11. Daily number of suspected bushfires in Western Australia detected from the NOAA-AVHRR satellite in 1995/96 by Remote Sensing Services, DOLA, whose location was reported to the Bush Fires Board within 4 hours of the overpass.

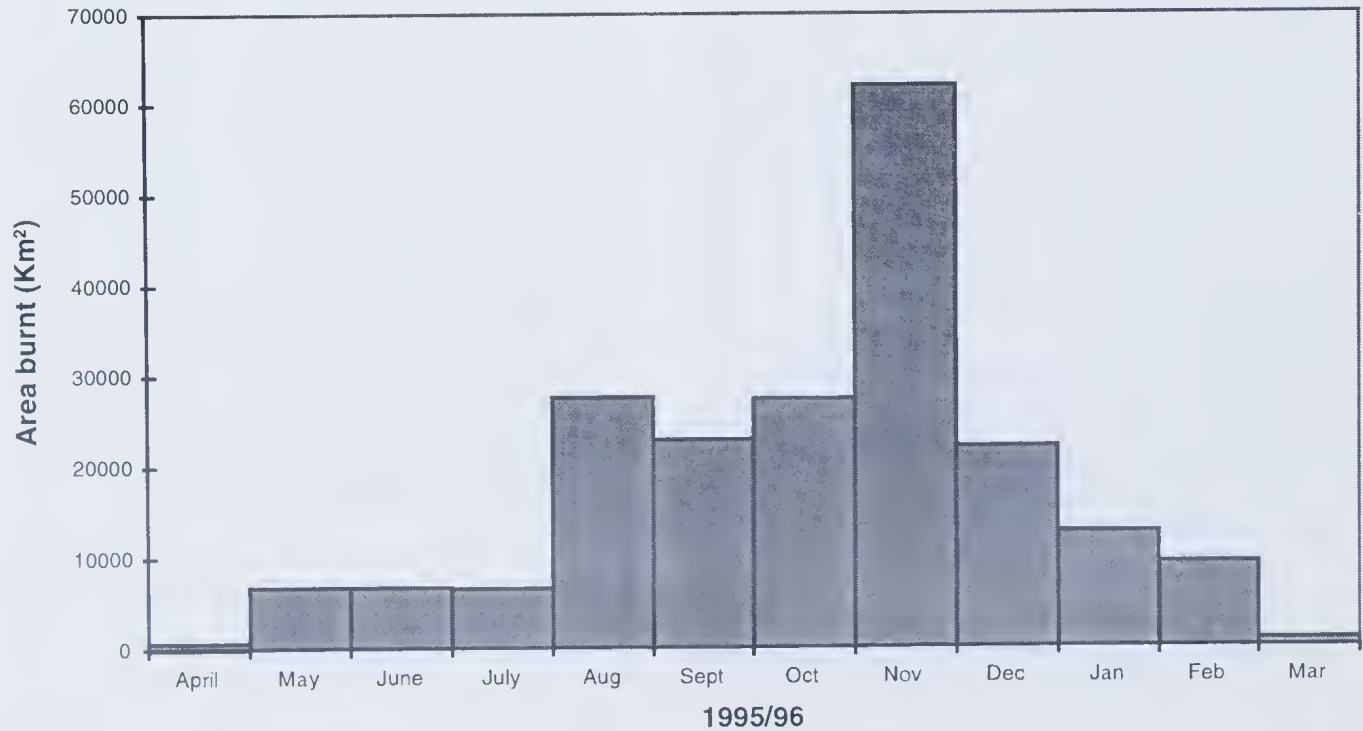


Figure 12. Area burnt by bushfires in Western Australia that was mapped from NOAA-AVHRR in 1995/96. Total area burnt is estimated at 20.6 million ha.

of over 2,700 bush fires reported to the Bush Fires Board by fax or internet within 4 hours of the data being received (Fig 11). The mapping indicated a total area burnt of about 20.6 million hectares, most in the north west of the State (Fig 12). This is the first time that such comprehensive information on bushfires has been available and is an example of the type of spatial and temporal geographic information that can now be made available from satellites.

The availability of these data on a routine basis in near real-time to the Bush Fires Board of Western Australia has had a significant impact on enrolling community support for the management of Bush Fires in the Kimberley. It has transformed a "we can do nothing" attitude to a "we can do". Instead of chasing bush fires, the Bush Fires Board reports that land managers are now able to see ahead and plan strategies that will provide more effective control and less risk.

Conclusions

Earth observations by satellite offers significant potential for using space to improve exploration and the management of Western Australia's renewable resources. After 20 years of research, techniques have progressed from the photo-interpretation of satellite imagery to the routine extraction of geographic information using automatic methods. The knowledge base for the much wider use of this technology has been created, but the challenge of widespread adoption remains.

Land cover types can be mapped and the spatial variability of certain key land surface processes measured from space. Monitoring changes in area of remnant native vegetation and salinity in the agricultural area using high resolution data, is now possible. Public access to such information provides a powerful means for Government to raise public awareness and support for extending the area of native vegetation. Application of NOAA-AVHRR to routinely monitor bush fires over West Australian has demonstrated that such systematic use of satellite information would improve the ability of Government to implement policies to combat environmental degradation.

Increased spatial, spectral and temporal resolution of future sensors will expand the opportunities for exploration and monitoring the environment. Ongoing Government investment into methods for capturing information from these new sensors, including X band reception capability in Western Australia for timely coverage may be required. Continued CSIRO research to generate the core knowledge to enable geographic information to be extracted from these new forms of data will be important.

The advent of ocean colour sensors and radar altimeters and radar scatterometers as a complement to existing sea surface temperature data will greatly enhance our ability to manage Western Australia's surrounding oceans and coastal zone.

We are at the beginning of the next era in earth observations from space which could give rise to many new applications of satellite remote sensing to the successful exploration and the management of the renewable resources of Western Australia.

Acknowledgements: The assistance and advice of members of the Leeuwin Centre for Earth Sensing Technologies and the WA Satellite and Technology Applications Consortium, and in particular staff of Remote Sensing Services, DOLA (previously RSAC, DOLA), CSIRO, World Geosciences Corporation, Curtin University of Technology and Bureau of Meteorology is greatly appreciated.

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A bibliography of research into satellite remote sensing of land, sea and atmosphere conducted in Western Australia

RCG Smith¹ & AF Pearce²

¹Remote Sensing Services, Department of Land Administration: richard_smith@notes.dola.wa.gov.au
and ²CSIRO Division of Marine Research: alan.pearce@marine.csiro.au
Leeuwin Centre for Earth Sensing Technologies, 65 Brockway Road, Floreat WA 6014

Manuscript received February 1997

Background to the bibliography

This bibliography on satellite and related remote sensing research in Western Australia covers both geological mapping for exploration and the monitoring of land, water, oceans and atmosphere. Publications related to exploration commissioned by the private sector and not publicly available have not been cited. The number of publications over time (Figure 1) reveals progressive development with alternate year peaks in recent years associated with the biennial Australasian Remote Sensing Conference.

The development of satellite remote sensing in Western Australia has been driven by the need of a small population to explore and manage efficiently a large and complex land surface. Western Australia's population of 1.7 million occupies a vast land area of 253 million hectares, with over 12,000 km of coastline and 40 million ha of continental shelf which covers part of Australia's exclusive

economic zone. The economy is dependent on mining and other primary industries, while environmental quality requires preservation of vegetative cover for maintaining bio-diversity and avoidance of desertification. Most of the land (93%) is under the ownership of the State. This State-owned land is allocated to conservation and timber extraction (17%), arid deserts, road reserves and foreshores (36%), pastoral grazing (37%), mining 3%, *etc.* Freehold land is only 7% and is used for agriculture (6%) and urban settlement (1%).

Unfortunately, 167 years of European settlement has caused much of the land, rivers and coastal waters to suffer degradation from bush fires, salinisation, erosion, disease, acidification, feral animals, eutrophication, siltation, pollution and resource depletion. Such degradation ranges from minimal to severe, but its actual extent and rate of spread is often not known because of the difficulty of monitoring the trends and changes over vast

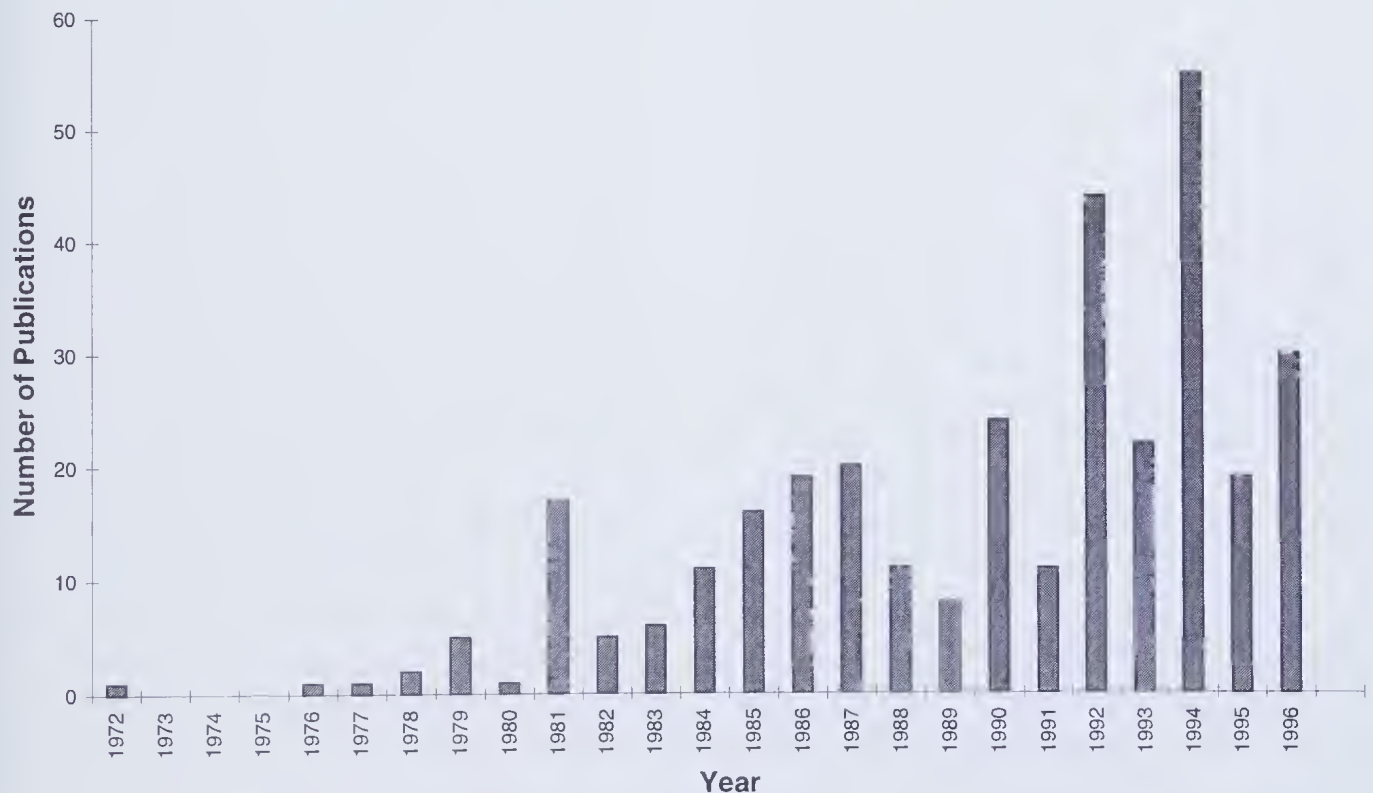


Figure 1. Progress of publications in remote sensing in Western Australia

areas. Absence of accurate information results in the problems being poorly managed. Therefore the Government in Western Australia needs access to comprehensive information on trends in land, water, atmosphere and coastal conditions to fulfill its environmental responsibilities. On land there is evidence of increasing use being made of satellite remote sensing to provide this information. Over the vast expanse of ocean there is evidence of use by marine scientists of satellite remote sensing for bathymetry, marine habitat mapping, estuarine water quality, ocean circulation and thermal structure, as well as by the fishing industry in fisheries operations. To maintain the continued discovery of new world class ore deposits under WA's deeply weathered regolith, new airborne geophysical and satellite remote sensing exploration techniques continue to be developed.

Commonwealth and State Government initiatives to capture the benefits of satellite remote sensing in Western Australia

The first operational earth resources satellite Landsat-1 was launched in 1971 and CSIRO formed a remote sensing group in Western Australia in 1974. CSIRO's initial emphasis was on spectral radiometry measurements in the visible and near infrared wavebands, which helped provide the bio-physical basis of multi-spectral remote sensing. Recognising the importance of multi-spectral data for mapping land surface features not captured by use of air photography, the WA Department of Lands and Surveys appointed remote sensing officers in 1975, who in 1983 formed the Remote Sensing Applications Centre (RSAC) within the Department of Lands and Surveys (later named Department of Land Administration, DOLA). Formation of RSAC focused remote sensing skills thus providing a resource base for the widespread use of this technology by a large number of Government agencies.

In the mid 1980s the CSIRO remote sensing group expanded as more disciplines saw research opportunities. Statisticians developed statistical classification of multi-spectral satellite data for mapping different land cover types and conditions. Geologists developed new satellite based methods to assist in geological mapping. Physicists applied space borne techniques for measurement of sea surface temperature and land surface evaporation. Biologists used satellites to measure biophysical variables from space such as biomass, crop yields and algal blooms. In contrast to the State's focus of its remote sensing efforts within DOLA, CSIRO's multi-disciplinary group is distributed across several Divisions and Institutes.

Universities

By the mid 1970s the first tertiary courses in remote sensing were being taught at the Western Australian Institute of Technology (later Curtin University of Technology) in the Schools of Electrical Engineering, Applied Physics, and Surveying and Land Information with assistance from CSIRO. One of the outcomes of this interaction was the development of an L band receiving station for the NOAA satellite. The first images were received in 1981, using a World War 2 bofors gun mount and oscilloscope to guide the receiving dish. This system was upgraded in 1987 and operations taken over by the WA Satellite Technology and Applications Consortium (WASTAC) of the Bureau of Meteorology, DOLA, CSIRO and Curtin University of Technology. Teaching of tertiary courses in satellite remote sensing now occurs in all WA Universities and at the College of Technical and Further Education (TAFE).

The Leeuwin Centre for Earth Sensing Technologies

Successful application of satellite remote sensing requires a diversity of skills. With scientists and funds scarce, early development of remote sensing in WA was marked by close collaboration between the different remote sensing groups within CSIRO, Curtin University, DOLA, Bureau of Meteorology and the private sector. In 1993, the importance of this collaboration was officially recognised when the Leeuwin Centre for Earth Sensing Technologies was built for \$5 million by the State Government on the CSIRO Floreat campus. The building co-located CSIRO's Remote Sensing Group, DOLA's Remote Sensing Services, Curtin University's Department of Applied Physics Remote Sensing Group, TAFE and World Geoscience Corporation, the largest airborne geophysical exploration company in the world.

The bibliography of papers, reports, theses and conference presentations listed here reveals a steady development in the application of satellite remote sensing to exploration and the management of Western Australia's renewable resources. The Leeuwin Centre brings together for the first time in Australia the three technologies of airborne geophysics, satellite remote sensing and geographic information systems. Co-location offers the opportunities to expand greatly the applications of satellite remote sensing through the synergy of the participating groups. After 20 years of development, WA now has for the first time the capability to map and monitor major environmental changes occurring in salinity, water quality, land productivity and native vegetation and use this information to enrol community support to tackle these problems. The challenge for these remote sensing groups is to create the synergy which will realise the full potential of the Leeuwin Centre and capture the benefits from the next generation of satellite sensors and associated technologies.

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Earth Sciences

Anand RR, Phang C, Wildman JE & Lintern MJ 1997 Genesis of some calcretes in the Southern Yilgarn Craton, Western Australia - implications for mineral exploration. *Australian Journal of Earth Sciences* 44:87-103.

A model for the genesis of pedogenic calcretes is developed by researchers from the CRC for Landscape Evolution and Mineral Exploration (CSIRO, Wembley), based on study of the Mt Gibson and Kalgoorlie regions. At Mt Gibson, calcrete is largely restricted to erosional regimes on greenstones and is absent or rare in relict and depositional regimes; in granitic terrain calcrete is absent in relict and erosional regimes but is present in minor amounts in depositional regimes. By contrast, it is present in all geomorphic regimes in the Kalgoorlie region although it is more abundant in erosional regimes on mafic bedrock. Ca and Mg in calcretes comes from *in situ* weathering, the dominant source in erosional regimes, and external sources, which have a larger input in depositional regimes. The differences in distribution of calcrete in relict and depositional regimes in the two study regions may be attributed to different conditions of weathering and landscape development.

Arne D 1996 Thermal setting of the Cadjebut Zn-Pb deposit, Western Australia. *Journal of Geochemical Exploration* 57:45-56.

Bau M, Hohndorf A, Dulski P & Beukes NJ 1997 S of rare-earth elements and iron in paleoproterozoic iron-formations from the Transvaal supergroup, South Africa - evidence from neodymium isotopes. *Journal of Geology* 105:121-129.

Boschetti F, Dentith MC & List RD 1996 Inversion of seismic refraction data using genetic algorithms. *Geophysics* 61:1715-1727.

Dickins JM 1996 Problems of a Late Palaeozoic glaciation in Australia and subsequent climate in the Permian. *Palaeogeography Palaeoclimatology Palaeoecology* 125:185-197.

Frey FA, McNaughton NJ, Nelson DR, De Laeter JR & Duncan R 1996 Petrogenesis of the Bunbury Basalt, Western Australia: interaction between the Kerguelen plume and Gondwana lithosphere. *Earth & Planetary Science Letters* 144:163-183.

Researchers from MIT, the University of Western Australia, Geological Survey of Western Australia, Curtin University and Oregon State University have collaborated to describe how subsequent to initial rifting of Greater India from Australia/Antarctica at ca 132 Ma, widespread Early Cretaceous volcanism occurred on the continental margins e.g. the ca 117 Ma Rajmahal Traps in northeast India and the ca 130-123 Ma Bunbury Basalt in the Perth Basin. The Bunbury Basalt can be divided into the 130 Ma Casuarina lavas and the 123 Ma Gosselin lavas. Sr and Nd isotopic ratios in Casuarina lavas are similar to those in younger lavas from the Ninetyeast Ridge and Kerguelen Archipelago which define the Kerguelen hotspot

track. Although the Bunbury Basalt may be a response to long-term incubation of the plume beneath eastern Gondwana, the eruption ages (130 and 123 Ma) are significantly older than the oldest measured ages (115-110 Ma) for the large igneous province (Kerguelen Plateau) associated with the plume when Western Australia was apparently ~1000 km from the plume. Hence the Bunbury Basalt may be unrelated to the plume and the geochemical similarities of Casuarina and younger plume-related lavas may be fortuitous.

Gray DJ, Schorin KH & Butt CRM 1996 Mineral associations of platinum and palladium in lateritic regolith, Ora Banda Sill, Western Australia. *Journal of Geochemical Exploration* 57:245-255.

Hamilton NTM & Collins LB 1997 Morphostratigraphy and evolution of a Holocene composite barrier at Minninup, southwestern Australia. *Australian Journal of Earth Sciences* 44:113-124.

The composite transgressive-regressive barrier system at Minninup differs substantially in morphology, stratigraphy and evolution from published barrier models. The Minninup barrier is characterised geomorphically by isolated back-barrier flats and channels, a broad, transgressive dune field, narrow foredune, reflective beach, and narrow and shallow nearshore zone. Stratigraphically, the mid- to late Holocene sandy barrier sediments are perched on top of muddy back-barrier facies. Mid-Holocene sea-level rise to approximately +3 m above present sea-level initiated development of raised beach and nearshore units. Heavy-mineral concentration has taken place throughout the development of the barrier and is preserved in all units.

Hubbard RNLB & Boulter MC 1997 Mid Mesozoic floras and climates. *Palaeontology* 40:43-70.

Johannesson KH, Lyons WB, Yelken MA, Gaudette HE & Stetzenbach KJ 1996 Geochemistry of the rare-earth elements in hypersaline and dilute acidic natural terrestrial waters - complexation behavior and middle rare-earth element enrichments. *Chemical Geology* 133:125-144.

Kang HJ & Fenical W 1997 Aplidiamine, a unique zwitterionic benzyl hydroxyadenine from the Western Australian marine ascidian *Aplidiopsis* sp. *Tetrahedron Letters* 38:941-944.

Kang HJ & Fenical W 1997 Ningalins a-d - novel aromatic alkaloids from a Western Australian ascidian of the genus *Didemnum*. *Journal of Organic Chemistry* 62:3254-3262.

Kent AJR & McDougall I 1996 Ar-40/Ar-39 and U-Pb age constraints on the timing of gold mineralization in the Kalgoorlie gold field, Western Australia - a reply. *Economic Geology & the Bulletin of the Society of Economic Geologists* 91:795-799.

Knight JT, Ridley JR, Groves DI & McCall C 1996 Syn-peak metamorphic gold mineralization in the amphibolite-facies, gabbro-hosted Three Mile Hill deposit, Coolgardie goldfield, Western Australia - a high-temperature analogue

- of mesothermal gabbro-hosted gold deposits. Transactions of the Institution of Mining & Metallurgy Section B-Applied Earth Science 105:B175-B199.
- Lintern MJ, Butt CRM & Scott KM 1997 Gold in vegetation and soil - three case studies from the goldfields of southern Western Australia. Journal of Geochemical Exploration 58:1-14.
- Mazzucchelli RH 1996 The application of soil geochemistry to gold exploration in the Black Flag Area, Yilgarn Block, Western Australia. Journal of Geochemical Exploration 57:175-185.
- Mishra HK 1996 Comparative petrological analysis between the Permian coals of India and Western Australia - paleoenvironments and thermal history. Palaeogeography Palaeoclimatology Palaeoecology 125:199-216.
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- Naldrett AJ 1997 Key factors in the genesis of Norilsk, Sudbury, Jinchuan, Voiseys Bay and other world-class Ni-Cu-pge deposits - implications for exploration. Australian Journal of Earth Sciences 44:283-315.
- Nemchin AA & Pidgeon RT 1997 Evolution of the Darling Range batholith, Yilgarn Craton, Western Australia - a SHRIMP zircon study. Journal of Petrology 38:625-649.
- Oliver NHS & Barr TD 1997 The geometry and evolution of magma pathways through migmatites of the Halls Creek Orogen, Western Australia. Mineralogical Magazine 61:3-14.
- Phillips GN, Groves DI & Kerrich R 1996 Factors in the formation of the giant Kalgoorlie gold deposit. Ore Geology Reviews 10:295-317.
- Researchers from Great Central Mines (Melbourne), the University of Western Australia, and the University of Saskatchewan, describe how Kalgoorlie (Golden Mile and Mt Charlotte) accounts for more than half of the gold obtained from the widespread gold mineralisation of the Archaean Yilgarn Craton and is one of the largest gold deposits in the world (>1800 t Au production and reserves). This giant gold deposit owes its size and unique position to a number of features of favourable host-rock composition, thickness and mechanical properties, favourable geometry of its host units and hosting greenstone belts at favourable PT conditions in the greenschist facies that together with proximity to the regional scale Boulder-Lefroy Fault allowed highly focused fluid flow on both a deposit and district scale.
- Rajesh HM, Santosh M & Yoshida M 1996 The felsic magmatic province in East Gondwana - implications for pan-African tectonics [Review]. Journal of Southeast Asian Earth Sciences 14:275-291.
- Reason CJC 1996 Topography and the dynamical response to easterly flow in southern hemisphere subtropical west coast regions. Meteorology & Atmospheric Physics 61:187-199.
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- Robinson BH, Chiarucci A, Brooks RR, Petit D, Kirkman JH, Gregg PEH & Dedominicis V 1997 The nickel hyperaccumulator plant *Alyssum bertolonii* as a potential agent for phytoremediation and phytomining of nickel. Journal of Geochemical Exploration 59:75-86.
- Seaman RS 1997 A comparison of some methods for reduction of pressure to sea level over Australia. Australian Meteorological Magazine 46:15-25.
- Seddon G 1996 Thinking like a geologist: the culture of geology. Mawson Lecture 1996. Australian Journal of Earth Sciences 43:487-495.
- Geology is described by G Seddon of the Centre for studies in Australian Literature (the University of Western Australia) as having a crucial role in both the scientific and popular culture. His conclusions regarding the nature of geology include: (i) there is no hierarchy of the sciences; (ii) geology is a Romantic science rather than a Classical one; (iii) there is no such thing as the scientific method; (iv) geologists often attempt to reconcile conflicting hypotheses; (v) geological phenomena are often of an almost irreducible complexity and their investigation is beset by problems of scale, both spatial and temporal; and (vi) the concept of universality has a distinctive application in geology. Among the non-professional uses of geology are: (i) human history is incomplete without environmental history; (ii) geology has application in environmental planning and management; and (iii) awareness of the geology of a region enhances the sense of place.
- Seitz HM & Keays RR 1997 Platinum group element segregation and mineralization in a noritic ring complex formed from proterozoic siliceous high magnesium basalt magmas in the Vestfold Hills, Antarctica. Journal of Petrology 38:703-725.
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- Coastal landforms along the arid Pilbara coast formed during the Quaternary through the influence of ancestral landforms and fluvial and shoreline accretion, coastal erosion, and cementation. Climate also played a significant role with high evaporation rates coupled with limited rainfall, cyclonic storms and limited sediment delivery to the coastal zone. As a result, this arid coast is characterised by a range of features such as construction of arid-zone deltas, delta destruction and sediment redistribution during times of sediment depletion, cyclone-induced erosion and sedimentation, mangrove deposits, formation of salt flats, and precipitation and cementation to form beachrocks, high tidal crusts and gypsum precipitates.
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- Siverson M 1996 Lamniform sharks of the mid Cretaceous Alinga Formation and Beedagong claystone, Western Australia. Palaeontology 39:813-849.
- Smith RE 1996 Regolith research in support of mineral exploration in Australia. Journal of Geochemical Exploration 57:159-173.
- Sugitani K, Horiuchi Y, Adachi M & Sugisaki R 1996 Anomalously low Al_2O_3/TiO_2 values for Archean cherts from the Pilbara Block, Western Australia - possible

evidence for extensive chemical weathering on the early earth. *Precambrian Research* 80:49-76.

Sundaralingam K 1997 Shear velocity structure beneath the Western Australian region. *Australian Journal of Earth Sciences* 44:69-75.

Sylvester P, Campbell IH & Bowyer DA 1997 Niobium/uranium evidence for early formation of the continental crust. *Science* 275:521-523.

Tompkins LA, Groves DI, Windrim DP, Jablonski W & Griffin WL 1997 Petrology, mineral chemistry, and exploration significance of Fe-sulfides from the metal dispersion halo surrounding the Cadjebut Zn-Pb mvt deposit, Western Australia. *Applied Geochemistry* 12:37.

Vanemden B, Thornber MR, Graham J & Lincoln FJ 1997 The incorporation of actinides in monazite and xenotime from Placer deposits in Western Australia. *Canadian Mineralogist* 35:95-104.

Vincent P 1996 Rillenkarren in the British Isles. *Zeitschrift für Geomorphologie* 40:487-497.

Williams GE 1997 Precambrian length of day and the validity of tidal rhythmite paleotidal values. *Geophysical Research Letters* 24:421-424.

Wilson TJ, Grunow AM & Hanson RE 1997 Gondwana assembly - the view from southern Africa and east Gondwana. *Journal of Geodynamics* 23:263-286.

Witt WK, Swager CP & Nelson DR 1996 Ar-40/Ar-39 and U-Pb age constraints on the timing of gold mineralization in the Kalgoorlie gold field, Western Australia - a discussion. *Economic Geology & the Bulletin of the Society of Economic Geologists* 91:792-795.

Woodhead JD & Hergt JM 1997 Application of the double spike technique to Pb-isotope geochronology. *Chemical Geology* 138:311-321.

Yeats CJ, McNaughton NJ & Groves DI 1996 Shrimp U-Pb geochronological constraints on Archean volcanic-hosted massive sulfide and lode gold mineralization at Mount Gibson, Yilgarn Craton, Western Australia. *Economic Geology & the Bulletin of the Society of Economic Geologists* 91:1354-1371.

Zhou HW 1996 A high-resolution p wave model for the top 1200 km of the mantle. *Journal of Geophysical Research-Solid Earth* 101(B12):27791-27810.

Life Sciences

Abensperg-Traun M, Arnold GW, Steven DE, Smith GT, Atkins L, Viveen JJ & Gutter M 1996 Biodiversity indicators in semi-arid, agricultural Western Australia. *Pacific Conservation Biology* 2:375-389.

A cooperative study by researchers from CSIRO Division of Wildlife Ecology (Midland) and the Agricultural University, Wageningen (Netherlands), investigated biodiversity indicators in semi-arid, agricultural Western Australia. Remnant area, vegetational structural diversity, species richness of plants, lizards and terrestrial arthropods, and the relative abundance of arthropod species were examined as indicators of faunal richness in two contrasting vegetation types, gimlet woodland and shrublands. No indicator variables effectively predicted total faunal richness for either vegetation type, but vegetation structural diversity and plant richness explained a

high percentage of variation in the richness of lizards, scorpions, termites and beetles in woodlands. The richness of the shrubland fauna was poorly predicted by all indicator variables. Differences in the predictive values of vegetation structure and plant richness between the two vegetation types was partly due to the spatial heterogeneity of biotic richness, and perhaps the scale of structure measurements.

Abensperg-Traun M, Steven D & Atkins L 1996 The influence of plant diversity on the resilience of harvester termites to fire. *Pacific Conservation Biology* 2:279-285.

Researchers from CSIRO Division of Wildlife Ecology (Midland) describe how the harvester termites of floristically-rich mallee-heath of southern Western Australia appear to be resilient to high-intensity fire, in contrast with harvesters in floristically-simple, intensely-burnt spinifex grassland of tropical Western Australia. It appears that high floristic diversity enhances the resilience of harvester termites to fire. Although the death of spinifex and associated harvester termites after fire may be atypical, the temporary local extinction of harvester termites might not be exceptional, particularly if the fire occurs with drought or high grazing pressure.

Agboma PC, Jones MGK, Peltonensainio P, Rita H & Pehu E 1997 Exogenous glycinebetaine enhances grain yield of maize, sorghum and wheat grown under two supplementary watering regimes. *Journal of Agronomy & Crop Science-Zeitschrift für Acker und Pflanzenbau* 178:29-37.

Akilan K, Marshall JK, Morgan AL, Farrell RCC & Bell DT 1997 Restoration of catchment water balance - responses of clonal river red gum (*Eucalyptus camaldulensis*) to water-logging. *Restoration Ecology* 5:101-108.

Amaoka K, Arai M & Gomon ME 1997 A new species of *Arnoglossus* (Pleuronectiformes, Bothidae) from the south-western coast of Australia. *Ichthyological Research* 44:131-136.

Anderson PK 1997 Shark Bay dugongs in summer. 1. Lek mating. *Behaviour* 134:433-462.

Bailey MC & Hamilton DP 1997 Wind induced sediment resuspension - a lake-wide model. *Ecological Modelling* 99:217-228.

Bray RA & Cribb TH 1997 Lepocreadiid (Digenea) species from members of the marine teleost family Cheilodactylidae from south-western Australia, including four new genera and five new species. *Systematic Parasitology* 37:27-45.

Carnegie AJ, Keane PJ & Podger FD 1997 The impact of three species of *Mycosphaerella* newly recorded on eucalyptus in western australia. *Australasian Plant Pathology* 26:71-77.

Chapman A & Lane JAK 1997 Waterfowl usage of wetlands in the south-east and interior of Western Australia 1992-93. *Emu* 97:51-59.

Cheeseman JM, Herendeen LB, Cheeseman AT & Clough BF 1997 Photosynthesis and photoprotection in mangroves under field conditions. *Plant Cell & Environment* 20:579-588.

Dawson TJ & Ellis BA 1996 Diets of mammalian herbivores in Australian arid, hilly shrublands: seasonal effects on overlap between euros (hill kangaroos), sheep and feral goats, and on dietary niche breadths and electivities. *Journal of Arid Environments* 34:491-506.

- Two researchers from the University of new South Wales describe the results of a 12 year study on the diets of euros (*Macropus robustus*), domestic sheep (*Ovis aries*) and feral goats (*Capra hircus*) in hilly shrubland of southern Australia. The diet of euros was based around grasses whereas grasses were important in the diet of sheep in wetter conditions but shrubs were important in the dry season. Feral goats had a broad diet, but a high preference for browse. Dietary niche breadths and electivities indicate only limited competition between the euros, sheep and goats.
- Eldridge MDB & Pearson DJ. 1997 Chromosomal rearrangements in rock wallabies, *Petrogale* (Marsupialia, Macropodidae). 9. Further g-banding studies of the *Petrogale lateralis* complex - *P. lateralis pearsoni*, the west Kimberley race, and a population heterozygous for a centric fusion. *Genome* 40:84-90.
- Field LH & Bailey WJ 1997 Sound production in primitive Orthoptera from Western Australia: sounds used in defence and social communication in *Ametrus* sp. and *Hadrogyllus* sp. (Gryllacrididae: Orthoptera). *Journal of Natural History* 31:1127-1141.
- Researchers from the University of Canterbury (New Zealand) and the University of Western Australia have collaborated to describe sound production in two undescribed Western Australian orthopteran insects (Gryllacrididae). Sound is used for both defence, produced by femoro-tergal stridulation, and intra-specific signalling by drumming on the substrate. The evolution of these calling behaviours is discussed with reference to the other primitive ensiferan family (Stenopelmayidae) known to produce both tergo-sternal defensive stridulation and femoral drumming.
- Kang HJ & Fenical W 1997 Aplidiamine, a unique zwitterionic benzyl hydroxyadenine from the Western Australian marine ascidian *Aplidiopsis* sp. *Tetrahedron Letters* 38:941-944.
- Kang HJ & Fenical W 1997 Ningalins a-d - novel aromatic alkaloids from a Western Australian ascidian of the genus *Didemnum*. *Journal of Organic Chemistry* 62:3254-3262.
- Loi A, Cocks PS, Howieson JG & Carr SJ 1997 Morphological characterization of mediterranean populations of *Biserrula pelecinus* L. *Plant Breeding* 116:171-176.
- Newell GR 1997 The abundance of ground-dwelling invertebrates in a Victorian forest affected by dieback (*Phytophthora cinnamomi*) disease. *Australian Journal of Ecology* 22:206-217.
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- Rahman MH & Hossain I Moslehuddin 1997 Nutritional evaluation of sweet lupin (*Lupinus angustifolius*) - net protein utilization (npu), nitrogen balance and fractionation studies. *British Journal of Nutrition* 77:443-457.
- Regan KL, Siddique KHM, Tennant D & Abrecht DG 1997 Grain yield and water use efficiency of early maturing wheat in low rainfall mediterranean environments. *Australian Journal of Agricultural Research* 48:595-603.
- Robinson BH, Chiarucci A, Brooks RR, Petit D, Kirkman JH, Gregg PEH & Dedominicis V 1997 The nickel hyperaccumulator plant *Alyssum bertolonii* as a potential agent for phytoremediation and phytomining of nickel. *Journal of Geochemical Exploration* 59:75-86.
- Siverson M 1996 Lamniform sharks of the mid Cretaceous Alinga Formation and Beedagong claystone, Western Australia. *Palaeontology* 39:813-849.
- Smolker R, Richards A, Connor R, Mann J & Berggren P 1997 Sponge carrying by dolphins (Delphinidae, *Tursiops* sp.) - a foraging specialization involving tool use. *Ethology* 103:454-465.
- Speers DJ & Jelfs J 1997 Typing of *Neisseria meningitidis* by restriction analysis of the amplified pora gene. *Pathology* 29:201-205.
- Steinborner ST, Wabnitz PA, Waugh RJ, Bowie JH, Gao CW, Tyler MJ & Wallace JC 1996 The structures of new peptides from the Australian red tree frog *Litoria rubella* - the skin peptide profile as a probe for the study of evolutionary trends of amphibians. *Australian Journal of Chemistry* 49:955-963.
- The Zoological Catalogue of Australia. Volume 28.** Strepsiptera (TR New), Mecoptera (KJ Lambkin), Neuroptera (TR New), Siphonaptera (AA Calder). The Australian Biological Resources Study, Canberra. CSIRO Publishing, Melbourne.
- Volume 28 of the outstanding monograph series by the Australian Biological Resources Study, *The Zoological Catalogue of Australia*, presents informative family introductions with generic and species synonymies, taxonomic information, status, distribution and ecological information, and bibliographies. The insect groups included in Volume 28 are Strepsiptera (42 species with a unique parasitoid existence), Mecoptera (30 endemic species that are important predators in natural systems and of biogeographic significance), Neuroptera (over 600 species that are important as biological control agents, with high endemism and fascinating archaic lineages), and Siphonaptera (80 valid species-group names with an impact on human health and disease, with high endemism and also exotics).
- Thompson GG & Withers PC 1997 Comparative morphology of Western Australian varanid lizards (Squamata: Varanidae). *Physiological Zoology* 233:127-152.
- This cooperative study by researchers from Edith Cowan University and the University of Western Australia considers intra-specific and interspecific changes in body shape with size, for 17 species of Western Australian goannas. Although goannas are generally considered to be conservative in shape, many body morphometric measurements were non-isometric, indicating significant variation in shape. Canonical variate analysis clearly differentiated the two subgenera of goannas (*Varanus* and *Odatia*) and species were generally sexually dimorphic. The morphological variation among the 17 goanna species was associated with foraging mode and ecology.
- Thompson GG & Withers PC 1997 Standard and maximal metabolic rates of goannas (Squamata: Varanidae). *Physiological Zoology* 70:307-323.
- Measurement of the standard and maximal metabolic rates of various Western Australian goannas, ranging in body mass from 10 to 3750 grams, by researchers from Edith Cowan University and the University of Western Australia indicated an unusual allometric effect of mass.

Standard metabolic rate was proportional to mass^{0.93 to 1.0}, with considerable variation between species, whereas maximal metabolic rate scales with mass^{0.79}. Consequently, the factorial metabolic scope is much greater for small goannas compared with large goannas. Inter-specific variation in metabolic physiology had some ecological correlates. Widely-foraging *Varanus tristis* and *V. eremias* had a high standard metabolic rate. Arboreal *V. caudolineatus*, *V. gilleni* and *V. tristis*, had a high maximal metabolic rate.

Tong SM 1997 Heterotrophic flagellates from the water column in Shark Bay, Western Australia. *Marine Biology* 128:517-536.

The diversity of heterotrophic flagellates in the water column at Shark Bay was examined by a researcher from the University of Sydney, and found to include 41 species of apusomonads, cercomonads, choanoflagellates, cryptomonads, euglenids, heteroloboseids, stramenopiles, and others of uncertain taxonomy. Three quarters of the species had not been previously reported from southern subtropical regions. It appears that many heterotrophic flagellates have a cosmopolitan distribution, and the biogeography of these Shark Bay species is discussed with regard to studies in other localities.

Wallace CC 1997 New species and new records of recently described species of the coral genus *Acropora* (Scleractinia, Astrocoeniina, Acroporidae) from Indonesia. *Zoological Journal of the Linnean Society* 120:27-50.

Williams ST & Benzie JAH 1997 Indo-west Pacific patterns of genetic differentiation in the high-dispersal starfish *Linckia laevigata*. *Molecular Ecology* 6:559-573.

Physical Sciences

Barton A 1997 States of Matter, States of Mind. IOP Publishing, USA.

This easy-to-read book introduces the structure and property of matter, how the physical world is put together and stays together. It explains some of the intricate details and some of the grand schemes of life, the universe, and everything, by making analogies with everyday experiences. Ranging from fundamental ideas and fundamental particles to the makeup of the universe, the contents of this book are understandable to readers with an inquiring mind but no scientific background. [available in Australia from DA Books: service@dadirect.com.au]

Clare BW & Supuran CT 1997 Carbonic anhydrase inhibitors. Part 41. Quantitative structure-activity correlations involving kinetic rate constants of 20 sulfonamide inhibitors from a non-generic series. *European Journal of Medical Chemistry* 32:311-319.

This collaborative research between Murdoch University and Università Degli Studi di Firenze (Italy) presents a quantitative structure-activity relationship for 20 sulfonamide inhibitors of carbonic anhydrase. These drugs, which are not of a classical congeneric series as the only common factor is the sulfonamide group, have as important local factors the Millikan charge on atoms of the sulfonamide group, and as global factors the size and shape of the molecule, calculated frontier orbital energies, and lipophilicity. The equilibrium constant and kinetic association rate were well correlated, but the kinetic dissociation rate constant was not.

Heftner G & Marcus Y 1997 A critical review of methods for obtaining ionic volumes in solution. *Journal of Solution Chemistry* 26:249-.

These researchers critically review the various methods for obtaining individual, or "absolute", ionic standard partial molar volumes from whole electrolyte data in aqueous and non-aqueous solutions. After revealing a number of undetected errors in previous analyses, it is shown that the reported agreement amongst the various methods in aqueous solution is largely fortuitous. Although all methods are unsatisfactory to varying degrees, the reference electrolyte approach, using an electrolyte such as tetraphenylarsonium, is the least objectionable. The researchers recommend that, at present, a difference between the standard partial molal volumes for Ph_4P^+ and BPh_4^- of $2 \text{ cm}^3 \text{ mol}^{-1}$ be used in all solvents at 25°C .

Kang HJ & Fenical W 1997 Aplidiamine, a unique zwitterionic benzyl hydroxyadenine from the Western Australian marine ascidian *Aplidiopsis* sp. *Tetrahedron Letters* 38:941-944.

Kang HJ & Fenical W 1997 Ningalins a-d - novel aromatic alkaloids from a Western Australian ascidian of the genus *Didemnum*. *Journal of Organic Chemistry* 62:3254-3262.

Obšil M, Majer V, Grolier J-PE & Heftner G 1996 Volumetric properties of, and ion-pairing in, aqueous solutions of alkali-metal sulfates under superambient conditions. *Journal of the Chemical Society, Faraday Transactions* 92:4445-4451.

Apparent molar volumes for $\text{Na}_2\text{SO}_4(\text{aq})$ and $\text{K}_2\text{SO}_4(\text{aq})$ have been obtained by collaborative densitometric research between Murdoch University and Université Blaise Pascal chemists, and from selected experimental data from the literature, at temperatures and pressures up to 573 K and 30 Mpa. Using the Pitzer ion-interaction model to correlate the data, the researchers obtained recommended values as a function of temperature and partial molar volumes at infinite dilution. Ion pairing was found to be significant for $\text{Na}_2\text{SO}_4(\text{aq})$ and $\text{K}_2\text{SO}_4(\text{aq})$ at higher temperatures.

Ralph DE & Stevenson JM 1995 The role of bacteria in well clogging. *Water Research* 29:365-369.

These researchers from Murdoch University studied the effect of ochreous sludge from blocked irrigation bores on the oxidation rate of soluble Fe(II). In comparison with sterile flasks of Fe(II) solution which showed the expected first order decline in Fe(II) concentration, flasks inoculated with ochreous sludge had significantly enhanced rates of Fe(II) oxidation, with the greatest increase at pH 8.5.

Robinson BH, Chiarucci A, Brooks RR, Petit D, Kirkman JH, Gregg PEH & Dedominicis V 1997 The nickel hyperaccumulator plant *Alyssum bertolonii* as a potential agent for phytoremediation and phytomining of nickel. *Journal of Geochemical Exploration* 59:75-86.

Steinborner ST, Wabnitz PA, Waugh RJ, Bowie JH, Gao CW, Tyler MJ & Wallace JC 1996 The structures of new peptides from the Australian red tree frog *Litoria rubella* - the skin peptide profile as a probe for the study of evolutionary trends of amphibians. *Australian Journal of Chemistry* 49:955-963.

Stelbovics AT & Berge L 1997 Nonuniqueness in the close-coupling method for *e*-He scattering. *Physical Review A* 55:1028-.

These researchers from Murdoch University present a general analysis of the close-coupling equations for e -He scattering and show why close-coupling expansion gives rise to nonunique solutions and are construct equations with a unique solution. The analyses concentrate on two models of target states, a frozen-core model with one electron restricted to the $1s$ He⁺ orbital, and a model using full configuration-interaction target states.

Thurgate SM 1996 Auger photoelectron coincidence experiments from solids. *Journal of Electron Spectroscopy and Related Phenomena* 81:1-31. [review]

Webb J, St Pierre T G, Tran KC, Chua-anusorn W, Macey DJ & Pootrakul P 1996 Biologically significant iron (III) oxyhydroxy polymers: Mössbauer spectroscopic study of ferritin and hemosiderin in pancreas tissue of β -thalassemia/hemoglobin E disease. *Inorganica Chimica Acta* 243:121-125.

Researchers from Murdoch University and Mahidol University (Thailand) used Mössbauer spectra of ferritin to show that it contained iron cores based on the ferrihydrite structure consistent with previous electron diffraction data. Cores in the crude hemosiderin are generally of this type, but some have a defective goethite structure.

Note from the Hon Editor: This column helps to link the various disciplines and inform others of the broad spectrum of achievements of WA scientists (or others writing about WA). References are abstracted from Current Contents by searching for Western Australia in the title and abstract.

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Diet of herbivorous marsupials in a *Eucalyptus marginata* forest and their impact on the understorey vegetation

K A Shepherd¹, G W Wardell-Johnson^{2,3}, W A Loneragan¹ & D T Bell¹

¹Department of Botany, The University of Western Australia, Nedlands WA 6907: email wal@cyllene.uwa.edu.au

²Manjimup Research Centre, Department of Conservation and Land Management, Brain Street, Manjimup WA 6258

³Current address: Botany Department, University of Namibia, Windhoek, Namibia: email gwardell@unam.na

Received April 1996; accepted February 1997

Abstract

Wire exclosures were established to exclude herbivores in remnant jarrah (*Eucalyptus marginata*) forest vegetation within the Perup Nature Reserve, south-western Australia, and were assessed after a 10 year period. Significantly higher plant cover values were recorded for a number of species protected from herbivory inside the exclosures compared to outside. Sub-shrubs and vines showed the greatest increase in vegetation cover within exclosures. *Bossiaea ornata*, *Billardiera variifolia*, *Opercularia hispidula*, *Logania serpyllifolia* and *Tetrarrhena laevis* were most favoured by herbivore exclusion in terms of relative abundance.

Faecal analysis confirmed that plant species having the greatest decrease in cover outside wire exclosures were consumed by one or more of the five predominant marsupial herbivores of the Perup forest. Faecal material collected over three sampling periods during 1992 revealed a total of 42 different plant species. The largest of the herbivores, the western grey kangaroo (*Macropus fuliginosus*), consumed the greatest diversity of plants (32 species in total), while the black-gloved wallaby (*Macropus irma*) and the tammar wallaby (*Macropus eugenii*) grazed 21 and 25 different species, respectively. The common brush-tail possum (*Trichosurus vulpecula*) consumed leaves from the two dominant trees of the region *Eucalyptus marginata* and *E. calophylla*, and four understorey species including *Leptomeria cunninghamii* and *Hakea lissocarpa*. Faecal samples of the western ring-tail possum (*Pseudocheirus occidentalis*) contained only forest canopy species.

This study has implications for appropriate flora and fauna management of nature reserves. Possible competition for plant resources was indicated by diet overlap. However, due to the polyphagous nature of these particular herbivores and an ability to shift resource preferences, competitive limitations of particular food resource species in the Perup Nature Reserve are unlikely. As herbivores have been shown to reduce plant cover in the area and, therefore, the rate of build up of fire fuels, their population management and potential impact in the Perup forest are important considerations for fire management plans in the forest.

Introduction

The Perup Nature Reserve (40000 ha; 34° 16' S, 116° 36' E) is located 45 km east of Manjimup in the south-west of Western Australia (Fig 1). The Perup forest is partially contiguous with other state forest lands, but is primarily surrounded by cleared farmlands. The Perup Nature Reserve is designated as a fauna management priority area (MPA) due to the documented presence of 21 species of native mammals, including at least five gazetted as rare or endangered (Christensen *et al.* 1985; Wardell-Johnson & Nichols 1991).

A knowledge of the range of plant life forms, leaf characteristics and species consumed by a diverse community of herbivores was considered desirable for greater understanding of individual dietary requirements, herbivore interactions and potential impact on vegetation. This would provide a basis for management

decisions on fuel reduction burns, habitat management fires and predator control.

This study had four aims. Firstly, to determine floristic differences between herbivore exclosures and adjacent open sites in the Perup Nature Reserve. Secondly, to document food resources utilised by the five major native herbivorous marsupials found within the area and determine possible factors influencing diet choice. Thirdly, to compare the findings from this study with other dietary studies of marsupial herbivores in reserves around the state and, finally, to assess possible management implications for the Perup Nature Reserve.

Materials and Methods

Study site

The topographic relief of the Perup Nature Reserve includes low undulating ridges separated by broad, flat valleys with seasonal swamps and streams in the lower

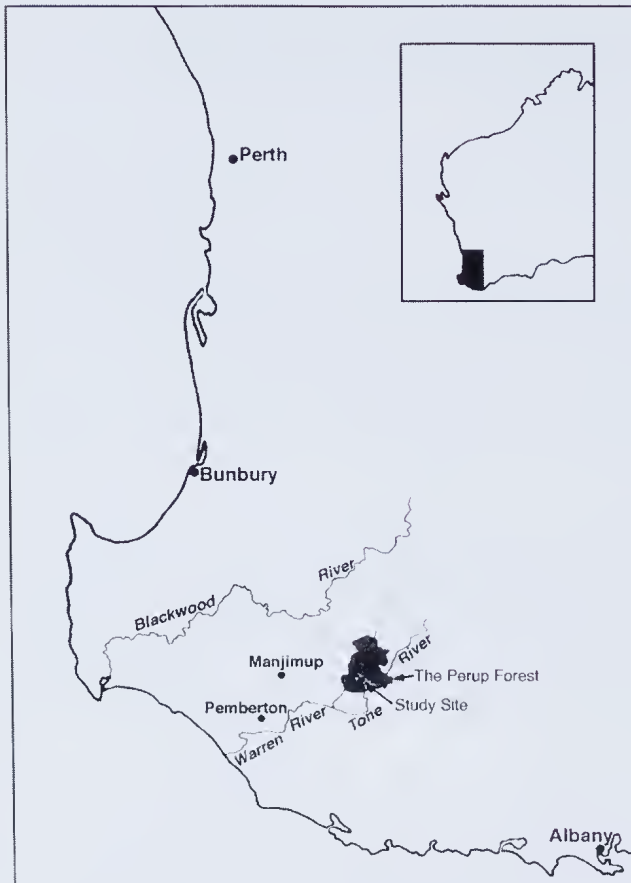


Figure 1. Location of the study site in the Perup Nature Reserve.

regions (Christensen 1980). The vegetation of the area is predominantly open jarrah (*Eucalyptus marginata*) along the ridges on lateritic soils, while marri (*Eucalyptus calophylla*) occurs more commonly in the valleys on the sandier soils. The understorey strata of the ridges and slopes are dominated by a diverse mixture of low (< 1 m) xeric shrubs with the common species being *Hakea lissocarpa*, *Leucopogon capitellatus* and *Bossiaea ornata*. Tall thickets (> 1m) form in some areas following a fire. These thickets are generally dominated by single species, either *Gastrolobium bilobum*, *G. spinosum*, *Melaleuca viminea* or *Acacia pulchella* (Christensen 1977; Buchanan & Wardell-Johnson 1990).

The Perup Nature Reserve was burnt frequently from the late 1930's to the mid 1960's. Cyclic fuel-reduction burning that is dependent on litter build-ups was initiated in the 1960's under the control of the Forest Department and subsequently the Department of Conservation and Land Management. More recently, it was recognised that a combination of intense autumn fires lit under dry soil conditions and milder spring fires was required to maintain the monospecific thickets and to stimulate the regrowth of the legume plant species (Christensen & Maisey 1987). In the presence of the European fox (*Vulpes vulpes*), these *G. bilobum* thickets are essential as refugia for the tamar population within the Perup forest (Christensen 1980).

Marsupial herbivore species

This study assessed the plant species consumed by five marsupial herbivores; the western grey kangaroo

(*Macropus fuliginosus*), the black-gloved wallaby (*Macropus irma*), the tamar wallaby (*Macropus eugenii*), the common brush-tail possum (*Trichosurus vulpecula*) and the western ring-tail possum (*Pseudocheirus occidentalis*). The western grey kangaroo (30-50 kg) has a wide distribution, extending from Western Australia across the continent to Victoria and central New South Wales (Poole 1983). The black-gloved wallaby is found only in the south-west of Western Australia (Christensen 1983). Although this large wallaby (7-9 kg) now occurs only in isolated populations, it is found in reasonable numbers within its natural range. The tamar wallaby, a smaller marsupial herbivore (5.5-7.5 kg), was once distributed over a diverse array of habitats prior to European settlement. This species is now gazetted as threatened and is restricted to a number of small isolated populations on coastal islands (Bell *et al.* 1987; Poole *et al.* 1991) and on the mainland of the south-west of Western Australia. The largest population on the mainland occurs in the Perup forest near dense *Melaleuca viminea* and *Gastrolobium bilobum* thickets which provide protection from predators such as foxes and feral cats (Christensen 1992). Populations of the common brush-tail possum occur in the forested regions of Western Australia and its distribution extends to eastern Australia (How 1983). The range of the western ring-tail possum is restricted to a few remnant jarrah forest and near-coastal *Agonis flexuosa* woodlands of the south-west of Western Australia (Jones *et al.* 1994a).

Exclosure methods

In autumn of 1981 following a prescribed burn, six wire-mesh exclosures were constructed along the eastern side of a 100 m section of the Glendale 2 Road, 1.5 km south of De Landgraaf Road in the Perup Nature Reserve (Inions *et al.* 1989). The exclosures were positioned along the upper to mid-slope of a broad valley within open jarrah/marri forest. The exclosures were approximately 1.5 m in height and 100 m² in area. They exclude all ground-dwelling mammals and it is unlikely that the arboreal possums gained access to the exclosed areas by traversing across the canopies of adjacent trees due to low canopy continuity at Perup. The possums are more likely to descend to ground level and walk to adjacent trees (Jones *et al.* 1994a). The area east of the Glendale 2 Road was subsequently burnt in 1984/1985 and the area to the west of the road was burnt in 1985/1986. In the winter of 1991, species cover within the six exclosures was determined along five, 10 m transects spaced 1 m apart using the point interception method (Mueller-Dombois & Ellenberg 1974). Pins were placed at 20 cm intervals along the transects (250 points per plot). Using the same methods, plant species cover values were also obtained for 19 open areas surrounding the exclosures. Mean cover values for the plant species inside and outside the wire exclosures were compared after arcsin transformation using a two-tailed Student's t-test.

Leaf epidermal material

A reference collection of prepared epidermal tissue slides of 67 species from the study site facilitated the microscopic identification of plant fragments recovered from faecal material. Epidermal vouchers were prepared using a modification of the acid digestion methods outlined

by Storr (1961) and Halford *et al.* (1984a). Leaf blades were covered in a 50% glacial acetic acid solution and heated in a water bath at 80 °C for 24-72 h. The fragments were then rinsed in water and any remaining fibrous tissue was removed. The cleared leaf fragments were then dehydrated through a series of ethanol solutions (increasing in concentration to 95%) and stained by immersion in 0.5% gentian violet in 95% alcohol for 48 h. The fragments were washed in 95% alcohol and mounted on slides using Eukit® permamount. Diagnostic line drawings of the epidermal tissue patterns, especially the guard cell complexes, were produced for each species as a further aid to identification.

Faecal material

Faecal pellets for each of the five common marsupial species in the area are distinctive in shape and size and can be easily separated by sight (P Christensen & C Wheeler, *pers comm*). Pellets were collected from a mid-slope area approximately 150 m by 500 m in the jarrah/marri open forest surrounding the exclosures. This area extended from the vicinity of the exclosures, down a westward facing slope into a low-lying gully. In contrast to the upper and mid-slope areas, large trees were absent in the gully being replaced by a dense thicket of *Gastrolobium bilobum* approximately 2 m in height. Fresh faecal pellets were collected over three sampling periods from the autumn through spring period of 1992.

The plant species consumed by the marsupial herbivores were determined by comparison of epidermal fragments in faecal material to the plant voucher specimens. However, a more rigorous digestion technique was required for preparation of the faecal pellets than for the plant vouchers. Single, air-dried faecal pellets were fragmented, placed in test tubes and covered with equal parts of 10% chromic acid and 10% nitric acid. The test tubes were heated in an acid digestion block at 80-100 °C within a fume hood, simmering the contents for 15-20 min. After maceration the contents were cooled to room temperature, and filtered with several washes of dilute potassium hydroxide solution and distilled water. The filtrate was sieved through a 0.5 mm sieve, collected and stained with 0.5% gentian violet in 95% alcohol. The fragmented plant material was scanned using the dissecting microscope at 12.5-50x magnification, mounted on slides with Eukit and compared with the voucher collection for species identification. As an index of dietary preference, the percentage occurrence of a plant species was determined by noting the proportion of the sampled pellets that included a particular plant species.

Results

A combined total of 73 plant taxa were recorded inside the exclosures and in the adjacent vegetation at the Perup Nature Reserve study site (Table 1). Nineteen species had significantly different and greater percentage cover values inside the wire exclosures. These included *Bossiaea ornata*, *Billardiera variifolia*, *Opercularia hispidula*, *Logania serpyllifolia*, *Tetrarrhena laevis*, *Scaevola striata* and *Billardiera floribunda*. Total plant cover outside the wire exclosures was only 58% of that recorded inside. In contrast, *Macrozamia riedlei*, *Eucalyptus marginata* and *Hibbertia commutata* had significantly greater cover values outside

the exclosures. Of the species showing a significant lower cover outside exclosures, 42% were small sub-shrub species, semi-woody or fibrous herbaceous perennials less than 0.5 m in height, and 26% were perennial vines and twining plants (Table 2).

Table 1

Plant cover values comparing wire exclosure treatments and adjacent open areas. * indicates significant difference by two-tailed t-test (≤ 0.05) following arcsin transformation. Plant classes: C, cycad; M, monocotyledon; D, dicotyledon. Life form: Tree, plant over 2 m height; Shrub, woody plant 0.5 - 2.0 m in height; Sub-shrub, semi-woody or fibrous herbaceous perennial < 0.5 m; Vine, twining perennial; Herb, mesophytic herbaceous perennial or annual.

Species	Percentage Cover		Plant Class	Life Form
	Inside	Outside		
<i>Bossiaea ornata</i>	24.6	4.0*	D	Shrub
<i>Billardiera variifolia</i>	13.8	1.2*	D	Vine
<i>Leucopogon capitellatus</i>	12.5	15.4	D	Sub-shrub
<i>Opercularia hispidula</i>	10.6	0.6*	D	Sub-shrub
<i>Logania serpyllifolia</i>	9.8	0.5*	D	Shrub
<i>Tetrarrhena laevis</i>	9.7	0.2*	M	Sub-shrub
<i>Hakea lissocarpa</i>	8.0	11.5	D	Shrub
<i>Xanthorrhoea gracilis</i>	7.7	6.4	M	Sub-shrub
<i>Drosera macrantha</i>	6.9	4.0	D	Herb
<i>Eucalyptus calophylla</i>	6.6	5.8	D	Tree
<i>Scaevola striata</i>	6.6	1.1*	D	Sub-shrub
<i>Billardiera floribunda</i>	6.2	0.2*	D	Vine
<i>Tricoryne elatior</i>	5.6	2.8	M	Sub-shrub
<i>Clematis pubescens</i>	5.1	0.9*	D	Vine
<i>Tetratheca affinis</i>	5.0	0.3*	D	Sub-shrub
<i>Chamaescilla corymbosa</i>	4.8	1.4*	M	Sub-shrub
<i>Lomandra caespitosa</i>	4.7	0.7*	M	Sub-shrub
<i>Leucopogon verticillatus</i>	4.3	4.4	D	Shrub
<i>Macrozamia riedlei</i>	4.1	9.7*	C	Shrub
<i>Eucalyptus marginata</i>	3.9	11.4*	D	Tree
<i>Hibbertia amplexicaulis</i>	3.5	4.5	D	Shrub
<i>Danthonia pilosa</i>	3.4	1.8	M	Herb
<i>Lageniphora huegelii</i>	3.2	1.3	D	Herb
<i>Cassytha</i> sp	3.0	0.0*	D	Vine
<i>Gastrolobium bilobum</i>	2.8	4.4	D	Shrub
<i>Pterostylis nana</i>	2.7	0.4*	M	Herb
<i>Leptomeria cunninghamii</i>	2.5	0.5*	D	Shrub
<i>Thysanotus patersonii</i>	2.4	0.0*	D	Vine
Grass A	2.1	1.3	M	Herb
<i>Xanthosia atkinsoniana</i>	2.0	1.1	D	Sub-shrub
<i>Agrostocrinum scabrum</i>	1.9	0.0*	M	Herb
<i>Lomandra preissii</i>	1.8	3.0	M	Sub-shrub
<i>Loxocarya fasciculata</i>	1.8	1.2	M	Sub-shrub
<i>Acacia pulchella</i>	1.5	1.1	D	Shrub
<i>Acianthus reniformis</i>	1.5	3.1	D	Herb
<i>Amphipogon</i>				
<i>amphipogonoides</i>	1.5	0.0*	M	Herb
<i>Lomandra integra</i>	1.5	0.5	M	Sub-shrub
<i>Xanthorrhoea preissii</i>	1.2	0.3	M	Shrub
<i>Caladenia repens</i>	1.2	0.7	M	Herb
<i>Comesperma confertum</i>	1.2	0.0*	D	Sub-shrub
<i>Leucopogon propinquus</i>	1.2	0.9	D	Sub-shrub
<i>Lomandra</i> sp #4	1.2	0.6	M	Sub-shrub
<i>Stackhousia monogyna</i>	1.2	0.0*	D	Sub-shrub
<i>Boronia spathulata</i>	0.6	0.9	D	Shrub
<i>Pimelea rosea</i>	0.6	0.4	D	Shrub
<i>Xanthosia candida</i>	0.6	0.4	M	Sub-shrub

Table 1 (continued)

Species	Percentage Cover		Plant Class	Life Form
	Inside	Outside		
<i>Acacia saligna</i>	0.0	0.1	D	Shrub
<i>Astroloma ciliatum</i>	0.0	0.1	D	Shrub
<i>Craspedia uniflora</i>	0.0	1.0	M	Herb
<i>Danthonia setacea</i>	0.0	0.3	M	Herb
<i>Daviesia preissii</i>	0.0	0.7	D	Shrub
<i>Hibbertia cunninghamii</i>	0.0	1.9	D	Shrub
<i>Hibbertia montana</i>	0.0	6.7*	D	Shrub
<i>Hibbertia racemosa</i>	0.0	0.3	D	Shrub
<i>Leucopogon australis</i>	0.0	1.0	D	Shrub
<i>Lomandra sericea</i>	0.0	0.2	M	Sub-shrub
<i>Lomandra sonderi</i>	0.0	0.2	M	Sub-shrub
<i>Lomandra</i> sp #1	0.0	0.7	M	Sub-shrub
<i>Lomandra</i> sp #2	0.0	0.2	M	Sub-shrub
<i>Loxocarya flexuosa</i>	0.0	0.2	M	Sub-shrub
<i>Melaleuca viminea</i>	0.0	0.4	D	Shrub
<i>Neurachne alopecuroides</i>	0.0	0.2	M	Herb
<i>Patersonia occidentalis</i>	0.0	0.8	M	Sub-shrub
<i>Pentapeltis peligera</i>	0.0	0.1	D	Herb
<i>Persoonia longifolia</i>	0.0	0.4	D	Tree
<i>Phyllanthus calycinus</i>	0.0	0.2	D	Shrub
<i>Stipa</i> sp	0.0	0.3	M	Herb
<i>Stylidium adnatum</i>	0.0	0.1	D	Herb
<i>Tetrariopsis octandra</i>	0.0	0.2	M	Sub-shrub
<i>Trachymene pilosa</i>	0.0	0.6	D	Herb
<i>Tremandra diffusa</i>	0.0	0.4	D	Sub-shrub
<i>Trymalium ledifolium</i>	0.0	0.3	D	Shrub
Dicotyledon #1	0.0	0.3	D	Shrub

Table 2

Plant life forms within the Perup study area (n = 73) and the percentage of life forms of the species showing potential of being selected by herbivores by recording a significantly lower cover outside the exclosures (n = 19).

	All Species	Reduced Value Species
Sub-Shrub	36	42
Shrub	31	16
Vine	7	26
Herb	22	16
Tree	4	0

Forty-two plant species in total were identified from the macropod faecal pellets, including both monocotyledonous and dicotyledonous species of varying life forms, together with 12 unidentified species (Table 3). Faeces of the largest of the herbivores, the western grey kangaroo, had 32 species in total, with a range of six to 13 different species found per faecal pellet (Fig 2). Analysis of the individual faecal pellets indicated that the sedge *Lepidosperma tenue* was an important dietary component for the western grey kangaroo, occurring in 89% of the pellets sampled (Table 3). Other species frequently consumed (occurring in $\leq 67\%$ of pellets sampled) included *Danthonia setacea*, an unknown monocotyledon (#1), *Gastrolobium bilobum* and a *Loxocarya* species. Sixteen

species were selected relatively infrequently, occurring in only 11% of the pellets sampled.

Table 3

Frequency of occurrence of plants recovered from herbivore faecal pellets collected in the Perup Nature Reserve. The plant species are ordered in approximate order of overall percentage.

	Western grey kangaroo	Black-gloved wallaby	Tammar wallaby	Brush-tail possum	Ring-tail possum
Monocotyledon #1	78	86	50		
<i>Danthonia setacea</i>	78	43	80		
<i>Gastrolobium bilobum</i>	67	43	50	40	
<i>Eucalyptus marginata</i>		14	17	60	100
<i>Hakea lissocarpa</i>	56	43	17	60	
<i>Loxocarya</i> sp	67	14	50		
<i>Bossiaea ornata</i>	33	86			
<i>Leucopogon capitellatus</i>	56	29	33		
<i>Lepidosperma tenue</i>	89		17		
<i>Acacia pulchella</i>	11	43	50		
<i>Eucalyptus calophylla</i>	11		67	20	10
<i>Leptomeria cunninghamii</i>			17	80	
Monocotyledon #2	11	43	33		
Dicotyledon #6		14	67		
Dicotyledon #1	44	29			
<i>Opercularia hispidula</i>	11	29	33		
<i>Juncus pallidus</i>	22	14	33		
<i>Cassytha</i> sp		29	33		
<i>Lomandra sericea</i>	11	14	33		
<i>Leucopogon verticillatus</i>	22	14	17		
<i>Tetraria octandra</i>			50		
Monocotyledon #3		14	33		
Monocotyledon #4	11		33		
<i>Boronia spathulata</i>	11	29			
<i>Daviesia preissii</i>	33				
<i>Lepidosperma angustatum</i>	33				
<i>Lomandra sonderii</i>			33		
Dicotyledon #5			33		
<i>Tetrarrhena laevis</i>	33				
<i>Billardiera variifolia</i>	11			20	
<i>Melaleuca viminea</i>	14	14			
Monocotyledon #5	11		17		
<i>Neurachne alopecuroides</i>	22				
<i>Centaureum erythraea</i>			17		
Dicotyledon #7		14			
<i>Astroloma ciliatum</i>	11				
<i>Kennedia carinata</i>	11				
<i>Lomandra</i> sp #3	11				
Dicotyledon #2	11				
Dicotyledon #3	11				
Dicotyledon #4	11				
Dicotyledon #8	11				

Twenty-one plant species were identified from the black-gloved wallaby pellets (Table 3), including four to nine plant species per sample (Fig 2). *Bossiaea ornata* and the unknown monocotyledon (#1) were frequent constituents of the black-gloved wallaby diet, being found in 86% of the pellets sampled. Other species were much less frequently consumed by wallabies, each species occurring in less than 43% of the pellets sampled.

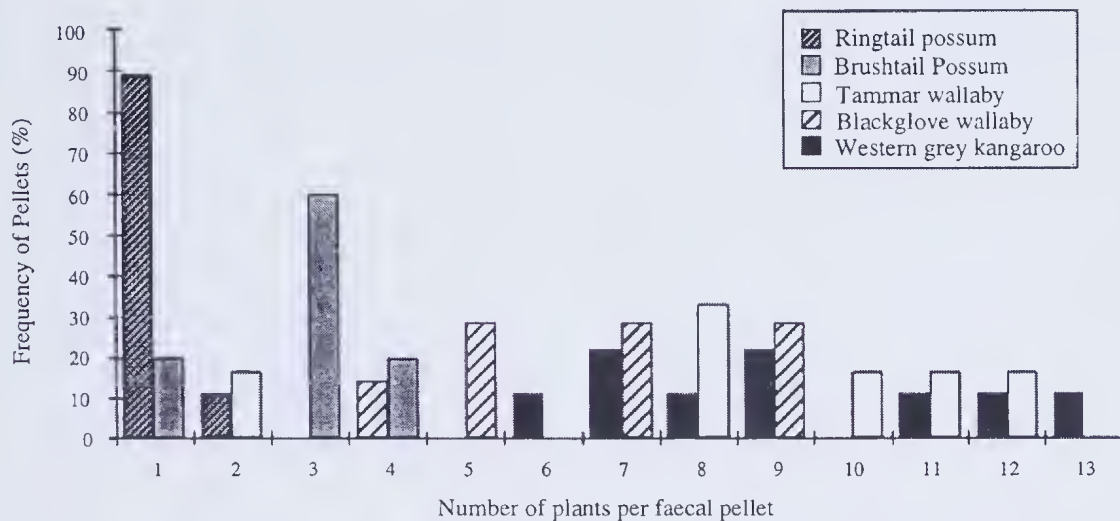


Figure 2. Frequency of plant species in sampled faecal pellets for the ring-tail possum, brush-tail possum, tammar wallaby, black-gloved wallaby and western grey kangaroo collected from the study site in the Perup Nature Reserve.

The diet of the tammar wallaby included 24 plant species in total (Table 3) with as many as 8-12 species recovered from single faecal pellets (Fig 2). One tammar faecal pellet, however, contained only two species. Plants most frequently consumed by this marsupial included *Danthonia setacea*, *Eucalyptus calophylla* and the unknown dicotyledon #6 recovered from 67-80% of the pellets sampled. Two other plant species frequently consumed, occurring in 50% of the pellets sampled, included the unknown monocot (#1) and the shrub *Gastrolobium bilobum*.

Of the plant species found in the faecal pellets, only 28% were consumed by all three macropods. The plant types ranged from the small restionaceous *Loxocarya* spp and the coarse, herbaceous sub-shrub *Opercularia hispidula*, to larger plants, such as *Juncus pallidus*. Species that have tough leaf spines as seen in *Hakea lissocarpha* and *Leucopogon capitellatus*, or stem spines as seen in *Acacia pulchella*, were also frequently grazed.

The arboreal possums appeared to consume fewer species than the macropods; also, fewer plant species were recorded per pellet during any one feeding period (Fig 2). The brush-tail possum diet consisted of six species (Table 3) with between one and four species per pellet (Fig 2). The most frequently consumed species included the understorey shrub *Leptomeria cunninghamii* and the two dominant tree species, *Eucalyptus marginata* and *E. calophylla*. Other understorey plants found in faecal material included the tall shrubs, *H. lissocarpha* and *G. bilobum*, and the vine *Billardiera variifolia*. Analysis of faecal pellets of western ring-tail possum revealed mainly *E. marginata* leaves, although fragments of *E. calophylla* were also retrieved from a single faecal sample. In addition to leaf epidermal fragments, pieces of seeds, bark and small insect larvae were also recovered from sampled pellets.

Discussion

After a ten-year period of herbivore exclusion, there was a floristic difference between the vegetation within

the exclosures and that of adjacent open sites in the Perup Nature Reserve. A number of species of various life forms had a significantly decreased vegetative cover when exposed to herbivory. Total plant cover was also much reduced outside the wire exclosures.

Dietary studies assist in understanding how herbivores utilise and subsequently influence their environment. Faecal analysis is an indirect but accurate means of determining the specific food resources consumed by herbivores (Scotcher 1979; Johnson & Pearson 1981; Holechek *et al.* 1982). The presence of cuticular material of plant species showing a decrease in vegetative cover in pellets collected from the five native herbivores within the Perup Nature Reserve, suggest that these herbivores have a significant impact on a broad range of species.

The Perup Nature Reserve is an important faunal reserve and an understanding of the resources required by the resident herbivores is essential to ensure appropriate management practices. The consumption of such a diverse array of species by the predominant herbivores may minimise the problem of overgrazing of any particular species. The ability of animal populations to selectively control relative densities of plant populations has been observed (Brown & Stuth 1993), but the complete elimination of a species or particular life forms from a natural ecosystem is unlikely. Murden & Risenhoover (1993), using additions of a known high-quality food supplement to assess the effects of forage quantity and quality on patterns of resource use, found that deer and goats continued to feed on a range of native plant species despite the presence of material of enhanced nutritional value. Their data suggest that normal behavioural patterns in large, free-ranging herbivores promote a polyphagous resource base, and thus reduce the probability of excessive utilisation pressure on any particular forage species. Although the marsupial herbivores of the Perup Nature Reserve showed particular preferences, the diversity of plant resources consumed indicates an ability to shift to other species when one plant species becomes less available. Increased emphasis on the land management practices designed preferentially for maintenance of the herbivores

in this Reserve, specifically maintaining stable population numbers, should not adversely affect the survival of particular plant species.

A comparison of plant species consumed by different herbivores potentially utilising the same food resource may give some indication of the interactions between herbivores and possible influences of diet choice. The overlap of plant species consumed by the large macropods indicates that there may be competition for resources in the Perup Nature Reserve. However, the herbivores tended to consume plants that were common in the understorey and, therefore, these are unlikely to become limiting. The polyphagous nature of these herbivores also allows them to graze a number of plant species at any one time, further limiting competition for specific plant resources.

The choice of plant species consumed may be influenced by a number of factors. Many researchers have tried to determine what specifically influences diet choice as it is unknown whether animals select items on the basis of nutritional content, avoidance of toxic compounds or physical deterrents, such as leaf and stem spines. The grazing of a diverse number of species as seen in the Perup marsupial herbivores may preclude problems of nutritional deficiency. Also, by consuming small amounts of plant material relatively infrequently, inherent multifunction oxidate detoxification systems may break down any novel toxins present (Dawson 1989). The herbivores of the Perup Nature Reserve do not appear to be deterred by the physiological and morphological defence characteristics that have evolved in Australian plants. These herbivores consumed species that have sharp stem spines (*Acacia pulchella*) and leaf spines (*Hakea lissocarpha*) or high concentrations of toxic compounds (*Gastrolobium bilobum* and *Eucalyptus* sp) (Freeland & Janzen 1974; Hume *et al.* 1984; Owen-Smith & Cooper 1987; Robbins *et al.* 1987). *Gastrolobium bilobum* contains up to 2600 mg kg⁻¹ of the toxic compound sodium fluoroacetate (King *et al.* 1981; Twigg & King 1991). The western grey kangaroo and the tammar are fluoroacetate-tolerant (Twigg & King 1991) and this study suggests that the black-gloved wallaby also has a high tolerance as this herbivore was found to commonly consume *Gastrolobium bilobum*.

Other factors such as inherent differences in body size may also influence diet choice as may behavioural learning by the grazers. Body size may also have influenced food choice in the Perup Nature Reserve accounting for differences in the total number of species consumed by the macropods and the possums. Small animals require more energy relative to body mass than do larger animals (Freudenberger *et al.* 1989). This means that larger herbivores generally have a diet of lower nutritive value and higher fibre content than do smaller herbivores. The faecal material of the western grey kangaroo collected in the Perup Nature Reserve contained a higher number of species per pellet compared to any of the other marsupial herbivores. The kangaroo is larger in size and may retain digested material for longer periods of time, thus increasing species richness within the digestive system. Smaller animals such as the brush-tail and ring-tail possums would be expected to have high metabolic rates and nutritional requirements; however, both species consumed

mostly *Eucalyptus* leaves which have a low nutritive value and contain toxic secondary compounds (Hume *et al.* 1984). The presence of several understorey species in the faeces of the common brush-tail possum indicates that this herbivore does not rely solely on the eucalypt canopy leaves as their only food resource. Both possum species may also supplement their diet with seeds, flowers and insect larvae. Ring-tail possums were found to have a very low field metabolic rate, much lower than expected for their body size (Hume *et al.* 1984). Due to the low metabolic rate these possums have lower total energy requirements, reflected in their decreased mobility compared to the more active brush-tail possums. The stomach of the western ring-tail possum is also well adapted to a folivorous diet, as it is simple in structure with a well developed caecum. This possum has a long gut retention time for its size (38-39 hours) allowing increased fermentation of the digestible material consumed. Low field metabolic rates of the ring-tail possum are reflected in low consumption rates, further minimising the consumption of the toxic compounds in the *Eucalyptus* foliage.

The differences in diet preference between individuals and between different species may also reflect behavioural learning and experience. Animals sample and continue to consume a range of species which they can tolerate while others may have encountered and subsequently utilise, a different range of plants (Bartmann & Carpenter 1982; Provenza & Balph 1987, 1988; Gillingham & Bunnell 1989). The results of these analyses allow a direct comparison of the food resources utilised by the macropod species within the Perup Nature Reserve to other populations found in the state. Of major interest is the consumption of predominantly dicotyledonous species by the western grey kangaroos. This is in contrast to the mixed diet of both dicotyledon and monocotyledon species recorded for populations of western grey kangaroos in pasture dominated landscape near Bakers Hill, Western Australia (Halford *et al.* 1984b; Bell 1993) and consumption of mainly monocotyledonous herbs in a *Banksia* woodland near Perth (Algar 1986). These differences in diet preference most likely reflect a difference in the predominance of these two subclasses as an available food source in the three study areas.

The dietary findings for the black-gloved wallaby in the Perup Nature Reserve were consistent with those of Algar (1986) who found a wide range of species in the diet, a majority of which were dicotyledons. He also recorded the consumption of tough sedge-like monocotyledons of the *Banksia* woodland habitat.

The tammar wallabies on Garden Island consumed a number of species, but preferred grasses or new shoots that appear following a burn (Bell *et al.* 1987). Christensen (1977) suggested that tammar wallabies in the Perup region rely almost entirely on the grasses associated with *Gastrolobium bilobum* thickets. It is evident from this study, however, that these wallabies consume a much wider range of species than those immediately associated with their daytime refugia. Thus, tammars require the maintenance of the more diverse vegetation of the upper slopes as well as the *Gastrolobium bilobum* thickets in the low lying areas.

The results from a dietary analysis by Jones *et al.* (1994b) of western ring-tail possum populations at Perup

and in isolated refugia of coastal vegetation in the south west of Western Australia indicated that the canopy foliage formed the main component of the possum diet. Pellets collected from regions of the Perup Nature Reserve away from the current study by Jones *et al.* (199b) also consisted of material of the two common canopy species, *Eucalyptus marginata* and *E. calophylla*. Analysis of pellets collected from coastal populations found that the common canopy species *Agonis flexuosa* dominated the possum diet selection (Inions *et al.* 1989).

The presence of a number of unknown plant species in the faecal material of all the macropods indicates that their foraging range extends beyond that of the immediate sampling site. Further study is essential to ensure establishment of appropriate management practices in Perup Nature Reserve to allow maintenance of marsupial herbivore population densities while considering the impact of grazing on surrounding vegetation. As all the marsupial herbivores utilise a number of common species and none of the macropods consume any single limited resource, it is unlikely that one group will out-compete another.

Fire management in native forests requires a knowledge of the accumulation of understorey vegetative material and leaf litter within specified areas. A measured decrease in the vegetative cover outside the exclosures independent of fire confirms the impact of herbivores on the vegetation of Perup Nature Reserve. The continued maintenance of stable herbivore populations will have implications for the reduction of plant cover and leaf litter buildup and may have benefits in allowing slightly increased fire intervals in the prescription burning regime for this forest. Thus an understanding of herbivore population numbers over time is essential as a marked increase in numbers can have an equally significant impact on the vegetation as would a sharp decline. These are important areas for further research and must be considered in the long-term management of this reserve.

Acknowledgments: Collection of data from the exclosures and surrounding vegetation was assisted by students in the 1992 course in Synecology. Scat identification was assisted by P Christensen and C Wheeler, Manjimup Research Centre, Department of Conservation and Land Management (CALM). Use of the Perup Forest Ecology Centre was provided by CALM during the period of the study. Special thanks also go to C Wilkins for her encouragement and invaluable comments.

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Dietary preferences of the black-gloved wallaby (*Macropus irma*) and the western grey kangaroo (*M. fuliginosus*) in Whiteman Park, Perth, Western Australia

J M Wann & D T Bell

Department of Botany, The University of Western Australia, Nedlands WA 6907: email dbell@cyllene.uwa.edu.au

Manuscript received April 1996; accepted February 1997

Abstract

Epidermal tissue trace analyses of faecal material indicated that the native banksia woodlands and adjacent managed grass areas of the Perth metropolitan Whiteman Park provided a varied diet for the black-gloved wallaby (*Macropus irma*) and the western grey kangaroo (*M. fuliginosus*). Black-gloved wallabies fed on a range of species, with a total of 29 included in the diet. *Cynodon dactylon*, the dominant grass of the lawn areas, *Carpobrotus edulis*, a succulent species in roadside disturbed sites, and the native cycad, *Macrozamia riedlei*, generally of the native woodland, were the three species most frequently consumed.

The diet of the western grey kangaroo included 25 species, with two grasses, *Cynodon dactylon* and *Ehrharta calycina*, the most frequently consumed. Western grey kangaroos showed a preference for monocotyledons, but dicotyledons also were common in the diet. Comparisons of thirteen chemical constituents and five morphological features of chosen and avoided plant species did not explain diet choice. A wide overlap of consumed plant species between the two herbivores indicated that competition for food resources was possible. However, the polyphagous diet for both species indicates that the ability to switch diet preferences probably precludes the competitive exclusion of one by the other.

Analysis of the epidermal material of the stomach, the small intestine, and the large intestine and colon indicated that the digestive system of the black-gloved wallaby did not completely remove plant epidermal traces of any of the ingested species. Therefore, the acid digestion technique used for faecal pellet analysis potentially indicates all the species consumed by the animal.

Retention of the mosaic of natural banksia woodland cover with adjacent areas of watered lawn should benefit the limited population of black-gloved wallabies in Whiteman Park. At present the population of western grey kangaroos is not large enough to consume enough material to affect either the population of black-gloved wallabies or the structural elements of the vegetation of Whiteman Park.

Introduction

Management programs are becoming increasingly important in the maintenance of wild animal populations. Land clearing and expansion of urban areas has resulted in small isolated remnants of bushland. Such 'remnant islands' are difficult for mammal populations to recolonise. Whiteman Park, in north-east metropolitan Perth, is such an 'island'. Whiteman Park is presently inhabited by two Macropodidae species, the black-gloved wallaby (*Macropus irma*) and the western grey kangaroo (*M. fuliginosus*). The population of black-gloved wallabies in the Park has been estimated at 40 animals (Arnold *et al.* 1991). The population of western grey kangaroos is much higher, at between 550 (Arnold *et al.* 1991) and 1000 animals (H Gratte, *pers comm*). Maintenance of these animals in the park is a priority, but little is known of their dietary preferences or the potential that one species might require the same resources and exclude the other.

Because of the low numbers of black-gloved wallabies in Whiteman Park, a non-destructive method of determining their dietary preferences was required. Procedures used to estimate the botanical composition of herbivore

diets include direct observation, utilisation techniques, analysis of mouth contents, fistula techniques, stomach analysis, and faecal analysis. Certain procedures are more useful than others, but each has important limitations. In this instance, faecal analysis was the preferred technique for these nocturnal macropods that often show severe stress when trapped. One road-killed black-gloved wallaby, however, afforded the opportunity to analyse digestive system contents and to provide a 'control' to the faecal pellet dietary samples.

The objectives of this study were to determine the plant species consumed by the black-gloved wallaby and the western grey kangaroo, to assess characteristics of favoured plants, and to determine the potential for resource competition between these two marsupial herbivores in the confined area of Whiteman Park.

Materials and Methods

Study site

Whiteman Park, comprising 2600 ha of natural bush and pasture, is situated approximately 20 km north-east of the central business district of Perth. The park is situated

on rolling sand dunes of the Bassendean soil association (Bettenay *et al.* 1960) over a portion of the important ground-water aquifer, the Gnangara Mound, that serves the metropolitan water supply (Anon 1992). The vegetation is a mixture of low woodland of *Banksia attenuata*, *B. menziesii* and *Eucalyptus tottiana* on upper slopes, grading through a taller woodland dominated by *E. marginata*, *E. calophylla* and *B. ilicifolia* to moist lowlands where a woodland of *Melaleuca preissiana* and *B. littoralis* occurs (Anon 1989). Stream margins in the southern end of the Park harbour an open forest dominated by *E. rudis* and *M. rhaphiophylla*.

Mammal study species

The black-gloved wallaby is a small wallaby (up to 9 kg), which is reported to graze rather than browse, and prefers a habitat of open forest or woodland (Christensen 1983). Due to its trap-shy nature and difficulty in handling, the black-gloved wallaby has rarely been studied. However, Shepherd *et al.* (1997) documented that the black-gloved wallabies in the Perup region of the southern jarrah forest consume at least 21 different plant species. Christensen (1983) also reported that they appear to be able to survive without free water. The black-gloved wallaby adds to the conservation value of Whiteman Park, especially since it is the nearest relative to the now extinct toolache wallaby (*Macropus greyii*). Although still common in a number of jarrah forest regions, the black-gloved wallaby is rare in the greater Perth urban region.

The western grey kangaroo is larger than the black-gloved wallaby, with males reaching 54 kg (Poole 1983). The western grey kangaroo both grazes and browses, and its diet has previously been shown to include a wide range of plant species and life-form types (Halford *et al.* 1984b; Priddel 1986; Bell 1994). Western grey kangaroos in a region of mixed wandoo-pasture country near Bakers Hill fed both on pasture species and a range of native plant species with some indication that nitrogen-rich legume species were selected in percentages greater than the percentages found as vegetative cover (Halford *et al.* 1984b). Western grey kangaroos in the Perup region of the southern jarrah forest consumed at least 32 different plant species, and marsupial herbivores appear to have the capacity to significantly reduce plant cover by their grazing pressure (Shepherd *et al.* 1997).

Plant resources

The detailed documentation of available plant resources for the two herbivore species was carried out in an area of approximately 700 ha in the northern region of Whiteman Park, where both marsupial herbivores have been observed. Detailed plant resource investigations were centred on three sites and covered a range of habitats. Site 1 was directly north and north east of the archery range parking lot. Site 2 included the archery range and the bushland to its east. Site 3 was approximately 300 m north-east of the International Trap and Skeet Shooting Complex. At each study site, percentage cover for each plant species was estimated for ten 2 m × 2 m quadrats placed along a randomly selected 20 m transect. Mean percentage cover and frequency of occurrence of each plant species were determined by combining the data for all three study transects, as the home ranges of both species would be larger than any one single site.

Fresh material was collected for moisture content, ash content and morphological characteristics for all plant species. It was stored in plastic bags inside an ice-filled cooler chest and returned to the laboratory within 2-3 h. Approximately 1 to 5 g of fresh leaf material was weighed, placed in paper bags, oven dried at 60 °C for 48 h, and re-weighed to determine percentage moisture content. Ash content was determined using dried plant material fired in a muffle furnace at 550 °C for 2 h. Dried leaf material from 82 plant species was analysed for 13 chemical constituents using flame spectrophotometry (CSBP & Farmers Ltd, Bayswater, Western Australia). Morphological characteristics of leaves from each plant species in the study area were determined from dried specimens. In plants with leaves absent or reduced, the morphological characteristics of stems or branches were determined. Five characteristics thought to influence feeding choice were summarised into the following categories;

- 1) apex type described the shape of the apices of leaves or branches/stems;
- 2) apex hardness separated all spine-tipped apices from soft-tipped, rounded, square-tipped and indented-tipped apices;
- 3) glands were noted as either present or absent;
- 4) leaf consistency scored as succulent, mesophyll, semi-sclerophyll or sclerophyll; and
- 5) both adaxial and abaxial tomentosity of leaves scored as either low, medium or highly pubescent or non-hairy.

These characteristics of plant species subsequently confirmed by faecal analysis as food resource species were compared to those of species not in faecal pellets using unpaired, two-tailed t-tests and coded chi-square tests. Such tests identify deviations from random and, therefore, can be used to determine if diet selection is occurring.

Epidermal reference collection

All plant species were collected at the study sites during the early autumn. Leaf material was used for the epidermal tissue reference collection for most species (see Halford *et al.* 1984a). For plants with phyllodes, cladodes or very reduced leaves, the petioles, stems, or branch materials (the materials that are potentially available as food for herbivores), were used for the epidermal reference collection.

Two methods were used to separate the epidermal material from the underlying tissues. The first, a modification of Jain (1976), involved placing 5 mm × 5 mm squares, or whole small leaves, in glass vials with 50% glacial acetic acid. The vials were placed in a water bath at 80 °C for 24-48 h, depending on the sclerophyllous nature of the material. On removal from the water bath, the plant material was washed with water and the remaining fibrous tissue was removed under a dissecting microscope using tweezers, dissecting needles and scalpel blades. The epidermal material was then dehydrated through a series of ethanol solutions to 95% and stained with 0.5% gentian violet in 95% ethanol for 48 h. The stained material was then rinsed in absolute alcohol and mounted in Eukitt®. The second technique, generally used for thicker material, employed a method similar to

that used by Storr (1961). Leaf material was placed in vials and covered with 10% chromic acid and 10% nitric acid, and boiled in an acid digestion heating block at 115 °C for 20-25 min. The tissue was then rinsed in 0.1 M KOH and the epidermal material was peeled off using tweezers and dissecting needles. The epidermal material was then dehydrated, stained and mounted as before.

Epidermal preparations were drawn to provide a visual record of the important characteristics of each plant species of the area.

Faecal sample collection and preparation

There was little difficulty in discriminating between the faecal pellets of black-gloved wallabies and western grey kangaroos. Faecal pellets of the former were smaller, round to oval, and pinched at the ends. Pellets of the latter were larger and at times almost cubic in shape. Fresh pellets were collected on a single day during each of the four seasons from the three vegetation study sites. Where there was more than one pellet in a deposit, only one was collected.

For each season, one pellet from each study site for each of the herbivores was randomly selected for fragment identification. Pellets were thoroughly dried, broken apart using tweezers, placed in a test tube and covered with 20 ml of equal parts 10% chromic acid and 10% nitric acid. The test tubes were placed in the acid digestion block in a fume hood and boiled at 115 °C for 20-25 min. The material was allowed to cool to room temperature before being filtered through a buchner funnel and Whatman No 10 filter paper with several washes of 0.1 M KOH. The filtrate was then collected and stained with 0.5% gentian violet in 95% alcohol for 48 h. After staining, the filtrate was passed through a 0.5 mm sieve and the remaining material was washed several times with 70% alcohol to remove excess stain. The tissue was placed in 95% alcohol in a glass petri dish and viewed through a dissection microscope at 6× to 30× magnification. Different species could generally be identified using the dissection microscope at its highest magnification. In some cases, a fragment was washed in absolute alcohol, mounted and viewed under a binocular microscope.

These epidermal fragments from faeces were then compared to the drawings of the epidermal reference collection and identification was confirmed by comparing the slide of the faecal epidermal fragment to the original plant voucher collection slide. Once a species had been positively identified, the proportion of each plant species in each pellet was subjectively determined as rare, common or abundant.

Black-gloved wallaby digestive tract contents

The carcass of an adult male black-gloved wallaby, killed on the road near the western boundary of Whiteman Park, was refrigerated within 5 h of its death. After 36 h in refrigeration, the digestive tract was removed and the stomach, small intestine and large intestine contents were separated. The large intestine and rectum contents could not be completely separated and were analysed together. The digestive contents were washed with water using a fine sieve to remove the digestive acids before being stored in alcohol. Epidermal tissue of the constituent plant species was obtained, stained and mounted using the methods described above.

Results

Plant resources available for herbivory

A total of 73 species were encountered in the transect samples, with mean cover ranging from more than 3% for *Patersonia occidentalis* to 0.01% for a number of species, such as *Adenanthos cygnorum*, *Arnocrinum preissii*, *Danthonia setacea* and *Oxylobium capitatum*, that were encountered only once (Table 1). The more common species included *Patersonia occidentalis*, *Xanthorrhoea preissii*, *Beaufortia elegans*, *Leucopogon conostephioides*, *Hypocalymma angustifolium* and *Alexgeorgea nitens*. Of the total species, 88% had a mean cover value less than 1%. No species was found in all 30 quadrats. *Gladiolus caryophyllaceus*, *Lyginia barbata*, *Hibbertia subvaginata* and *Patersonia occidentalis* had the highest frequency values, ranging from 85% to 62%. Of the total species, 24% were found in only a single quadrat.

Black-gloved wallaby digestive tract contents

A total of eight species (seven dicotyledons and one monocotyledon) were identified in the stomach and intestinal tract of the road-killed black-gloved wallaby

Table 1

Mean percentage cover in quadrats and percentage frequency of plant species in the 30 quadrats sampled in Whiteman Park (see text for quadrat locations).

Species	Percentage Cover	Percentage Frequency
<i>Patersonia occidentalis</i>	3.03	62.5
<i>Xanthorrhoea preissii</i>	2.95	35.0
<i>Beaufortia elegans</i>	2.20	32.5
<i>Leucopogon conostephioides</i>	2.15	37.5
<i>Hypocalymma angustifolium</i>	2.02	15.0
<i>Alexgeorgea nitens</i>	1.86	60.0
<i>Eremaea pauciflora</i>	1.70	22.5
<i>Lyginia barbata</i>	1.29	70.0
<i>Calytrix angulata</i>	1.25	32.5
<i>Hibbertia subvaginata</i>	0.93	70.0
<i>Stirlingia latifolia</i>	0.92	27.5
<i>Lechenaultia floribunda</i>	0.70	15.0
<i>Schoenus curvifolius</i>	0.49	40.0
<i>Dampiera linearis</i>	0.49	30.0
<i>Hibbertia hypericoides</i>	0.45	22.5
<i>Henriandra linearis</i>	0.45	12.5
<i>Conostephium pendulum</i>	0.44	30.0
<i>Dasyopogon bromeliifolius</i>	0.42	20.0
<i>Scholtzia involucreata</i>	0.36	22.5
<i>Gompholobium tomentosum</i>	0.36	20.0
<i>Stylidium repens</i>	0.35	32.5
<i>Acacia pulchella</i>	0.33	20.0
<i>Hypocalymma robustum</i>	0.31	17.5
<i>Calytrix flavescens</i>	0.30	22.5
<i>Allocasuarina fraseriana</i>	0.30	5.0
<i>Banksia attenuata</i>	0.25	7.5
moss	0.24	27.5
<i>Loxocarya flexuosa</i>	0.24	20.0
<i>Stipa</i> sp	0.20	15.0
<i>Banksia ilicifolia</i>	0.20	7.5
<i>Melaleuca preissiana</i>	0.18	2.5
<i>Trachymene pilosa</i>	0.15	32.5
<i>Hibbertia huegelii</i>	0.15	12.5

Table 1 (continued)

Species	Percentage Cover	Percentage Frequency
<i>Gladiolus caryophyllaceus</i>	0.13	85.0
<i>Petrophile linearis</i>	0.13	12.5
<i>Airia</i> sp	0.12	5.0
<i>Bossiaea eriocarpa</i>	0.09	17.5
<i>Waitzia podolepis</i>	0.09	17.5
<i>Acacia sessilis</i>	0.09	15.0
<i>Jacksonia floribunda</i>	0.08	10.0
<i>Leucopogon polymorphus</i>	0.08	10.0
<i>Briza maxima</i>	0.08	5.0
orchid spp	0.07	20.0
<i>Eriostemon spicatus</i>	0.06	17.5
<i>Banksia menziesii</i>	0.06	15.0
<i>Drosera erythrorhiza</i>	0.05	25.0
<i>Pimelea sulphurea</i>	0.05	5.0
<i>Persoonia saccata</i>	0.05	5.0
<i>Daviesia triflora</i>	0.05	2.5
<i>Scaevola paludosa</i>	0.05	2.5
<i>Acacia stenoptera</i>	0.03	2.5
<i>Burtonia scabra</i>	0.03	2.5
<i>Calectasia cyanea</i>	0.03	2.5
<i>Hibbertia racemosa</i>	0.03	2.5
<i>Regelia ciliata</i>	0.03	2.5
<i>Ehrharta calycina</i>	0.02	20.0
<i>Haemodorum spicatum</i>	0.02	17.5
<i>Drosera macrantha</i>	0.01	10.0
<i>Ursinia anthemoides</i>	0.01	7.5
<i>Allocasuarina humilis</i>	0.01	5.0
<i>Hypochaeris glabra</i>	0.01	5.0
<i>Lepidosperma angustatum</i>	0.01	5.0
<i>Stylidium brunonianum</i>	0.01	5.0
<i>Thysanotus</i> sp	0.01	5.0
<i>Adenanthos cygnorum</i>	0.01	5.0
<i>Anizoganthos humilis</i>	0.01	2.5
<i>Arnocrinum preissii</i>	0.01	2.5
<i>Banksia grandis</i>	0.01	2.5
<i>Danthonia setacea</i>	0.01	2.5
<i>Lomandra hermaphrodita</i>	0.01	2.5
<i>Oxylobium capitatum</i>	0.01	2.5
<i>Tricoryne elatior</i>	0.01	2.5
rhizomatous monocotyledon	0.01	2.5

Table 2

Plant species identified in the stomach, small intestine and large intestine of a road-killed black-gloved wallaby. The subjective scale of fragment abundance in the samples is rare (R), common (C), abundant (A) and not recorded (x). Unknown dicotyledons #8 and #9 were not included in the voucher collection from the study site.

Species	Stomach	Small Intestine	Large Intestine
<i>Adenanthos cygnorum</i>	R	R	R
<i>Arnocrinum preissii</i>	C	C	C
<i>Eriostemon spicatus</i>	C	C	C
<i>Hovea trisperma</i>	C	C	C
<i>Nuytsia floribunda</i>	R	R	R
<i>Leucopogon conostephioides</i>	R	R	x
dicotyledon #8	C	C	C
dicotyledon #9	C	C	C
Total Species Identified	8	8	7

(Table 2). Seven plant species were identified from all three parts of the digestive tract. *Leucopogon conostephioides* was present in very small quantities in the stomach and small intestine, but was not identified recorded for the large intestine. The similarity of species content throughout the digestive tract confirmed that faecal pellet analysis provides a sufficiently accurate indication of these plant species.

Black-gloved wallaby faecal pellets

Twenty-nine plant species were recovered from the black-gloved wallaby faeces collected at Whiteman Park (Table 3). On average, six to seven plant species were found in each pellet, and season had no effect on the number of plant species consumed. Of the 29 species consumed, 21 were positively identified using the epidermal reference collection. The remaining eight (seven dicotyledon species and one monocotyledon species) were not able to be identified to species. Three of the 21 identified species consumed were the succulent exotic *Carpobrotus edulis* and the two introduced grasses *Cynodon dactylon* and *Ehrharta calycina*. *Carpobrotus edulis* was especially common in all faecal pellets during summer and autumn, but was absent from the pellets in winter and spring. *Cynodon dactylon* is the grass used in the managed and watered lawn areas of the archery and skeet shooting ranges. *Ehrharta calycina* is especially common in disturbed areas along the roads and parking lots.

The most common native species in the black-gloved wallaby diet was *Macrozamia riedlei*, occurring in 50% of the faecal pellets analysed. *Tricoryne elatior* was found in 42% of the pellets, while *Leucopogon conostephioides*, *Nuytsia floribunda* and the unknown dicotyledon #1 were found in 33% of the pellets examined. Eleven species, including *Patersonia occidentalis*, *Conostephium pendulum* and *Mesomelaena stygia*, were found in only a single pellet. *Carpobrotus edulis*, *Cynodon dactylon*, *Nuytsia floribunda* and unknown dicotyledon #1 were the only species classed subjectively as abundant in one or more faecal pellets. The remaining 25 species were classified as either common or rare in faecal pellets. All but one of the species consumed (*Macrozamia riedlei*) belong to the class Magnoliopsida. Of these, 64% were dicotyledons and 36% were monocotyledons. This compares to the 69% dicotyledons:31% monocotyledons proportions noted for the ratio found in the vegetation survey.

Western grey kangaroo faecal pellets

Twenty-five species were represented in the faecal pellet samples of the western grey kangaroo of Whiteman Park (Table 4). An average of six plant species was found per pellet over the entire year, with no obvious seasonal pattern observed in the number of species in each sample. Of the 25 species identified in the faecal material, 20 species were identified using the epidermal reference collection. The same three exotic species consumed by the black-gloved wallabies were found in the pellets of the western grey kangaroos. *Carpobrotus edulis* was found in 42% of the pellets examined, and was common to abundant in most of the pellets in all seasons except spring. *Cynodon dactylon* was the most frequently consumed exotic species, occurring in 58% of the faecal pellets.

The tufted perennial *Alexgeorgea nitens* was the most commonly identified native species, occurring in 75% of the samples. Other native species commonly identified in

Table 3

Plant species identified in black-gloved wallaby faecal pellets collected during the four seasonal sampling periods. Three pellets were analysed during each sampling period. The subjective scale of fragment abundance in the pellet is rare (R), common (C) and abundant (A). Percentage of occurrence (%) for all sample pellets (n=12) through the year, and the total species richness in each sample pellet, are shown.

Plant Species	Site	Summer			Autumn			Winter			Spring			%
		1	2	3	1	2	3	1	2	3	1	2	3	
<i>Acacia stenoptera</i>							R		R					17
<i>Alexgeorgea nitens</i>											C			8
<i>Arnocrinum preissii</i>									R					8
<i>Beaufortia elegans</i>								R	C			R		25
<i>Carpobrotus edulis</i>		A	A	C		R	C	C						50
<i>Conostephium pendulum</i>													R	8
<i>Corynotheca micrantha</i>			C					R						17
<i>Cynodon dactylon</i>		C	C	A		A	C	A	C		C	C	C	83
<i>Dampiera linearis</i>					R						R			17
<i>Danthonia setacea</i>						R		R						17
<i>Ehrharta calycina</i>				R								R		17
<i>Eucalyptus marginata</i>												R		8
<i>Leucopogon conostephioides</i>					R					R		C	C	33
<i>Leucopogon</i> sp A											C	C	C	25
<i>Lysinema ciliatum</i>			R											8
<i>Macrozamia riedlei</i>		R	R	C			R					C	R	50
<i>Mesomalaena stygia</i>		R												8
<i>Nuytsia floribunda</i>								A	R	A		R		33
<i>Oxylobium capitatum</i>						R			R					17
<i>Patersonia occidentalis</i>							R							8
<i>Tricoryne elatior</i>		C		C		C		C		C				42
dicotyledon #1					A	A	A				C			33
dicotyledon #2						C	R			R				25
dicotyledon #3				R										8
dicotyledon #4									C					8
dicotyledon #5									C					8
dicotyledon #6								R	R					17
dicotyledon #7							R							8
monocotyledon #1		C		C			C							25
Total Species Richness		6	5	7	5	7	9	7	8	4	5	8	5	

the western grey kangaroo faecal material included *Leucopogon* sp A, *Leucopogon conostephioides*, *Danthonia setacea*, *Corynotheca micrantha* and *Dampiera linearis*. Of the 24 angiosperm species in the diet, 58% were dicotyledonous species and 42% were monocotyledonous species. As for the black-gloved wallaby, the faecal pellets of the western grey kangaroo tended to contain a number of species of plants with few being in abundant concentrations.

Diet overlap

Both the black-gloved wallaby and the western grey kangaroo were versatile feeders, consuming a wide range of plant species. There was considerable overlap in the feeding preferences, with 18 species consumed by both macropods. Species that frequently appeared in the faecal pellets of both animals included *Carpobrotus edulis*, *Cynodon dactylon*, *Leucopogon conostephioides* and *Leucopogon* sp A. Some species were in a large proportion of the faecal pellets from one macropodid, but only in one or two pellets from the other species. For example, *Alexgeorgea nitens* occurred in 75% of the western grey kangaroo faecal pellets but only 8% of the black-gloved wallaby faecal pellets. Other species such as *Ehrharta*

calycina, *Oxylobium capitatum* and *Patersonia occidentalis*, were in only one or two faecal pellets from both macropods.

Food resource characteristics

The plant species consumed by black-gloved wallabies had a mean field cover of 0.43% compared to a mean cover of 0.24% for those not consumed, but the difference was not significant (Table 5). Similarly, mean percentage covers of the consumed and non-consumed species were not significantly different for the diet selected by the western grey kangaroos. Of the thirteen chemical constituents considered, there were no significant differences observed between the mean content in plants eaten and those not eaten by the black-gloved wallaby for any of the comparisons. Results were similar for the western grey kangaroo, except nitrate in dietary resources was significantly higher in the plants chosen compared to the plants avoided. Moisture content was not significantly different for plant species consumed and avoided, for either macropod. The ash content of the plants chosen and avoided were also not significantly different for the diets of either species.

Table 4

Plant species identified in western grey kangaroo faecal pellets collected during the four seasonal sampling periods. Three pellets were analysed during each sampling period. The subjective scale of fragment abundance in the pellet is rare (R), common (C) and abundant (A). Percentage of occurrence (%) for all sample pellets (n=12) through the year, and the total species richness in each sample pellet, are shown.

Plant Species	Site	Summer			Autumn			Winter			Spring			%
		1	2	3	1	2	3	1	2	3	1	2	3	
<i>Adenanthos cygnorum</i>		R		C				R						25
<i>Alexgeorgea nitens</i>		C		C	C	R	C	C		C	C		C	75
<i>Bossiaea eriocarpa</i>								R			R			17
<i>Carpobrotus edulis</i>		C		C		C	C			A				42
<i>Conostephium pendulum</i>			C								C			17
<i>Corynotheca micrantha</i>			R						R		C		R	33
<i>Cynodon dactylon</i>		C	C	C		C			A		C		C	58
<i>Dampiera linearis</i>			R	R		R	C							33
<i>Danthonia setacea</i>								C		C	C	C	C	42
<i>Ehrharta calycina</i>		R			A									17
<i>Jacksonia furcellata</i>											R			8
<i>Leucopogon conostephioides</i>			C			C		C		C				33
<i>Leucopogon</i> sp A					C			C	R		C	C	R	50
<i>Loxocarya flexuosa</i>												R		8
<i>Macrozamia riedlei</i>								R		C				17
<i>Nuytsia floribunda</i>		C												8
<i>Oxylobium capitatum</i>			C				R							17
<i>Patersonia occidentalis</i>												R		8
<i>Stipa</i> sp A												R		8
<i>Tricoryne elatior</i>			C											8
dicotyledon #1		C				C								17
dicotyledon #4				R										8
dicotyledon #7				C		C	C		C					33
dicotyledon #8												R		8
monocotyledon #2											R			8
Total Species Richness		7	7	7	3	7	5	7	4	5	9	6	5	

Table 5

Characteristics of species chosen (those positively identified in faecal material) and those avoided (those not confirmed in faecal material) in the diets of the black-gloved wallaby and western grey kangaroo populations in Whiteman Park. NS is not significant.

Characteristic	Black-gloved wallaby				Western grey kangaroo			
	Chosen	Avoided	t or χ^2	Sig. Diff.	Chosen	Avoided	t or χ^2	Sig. Diff.
Field vegetation								
Field Cover (%)	0.43 ± 0.18	0.24 ± 0.06	1.33	NS	0.42 ± 0.19	0.25 ± 0.06	1.07	NS
Plant Frequency (%)	12.81 ± 3.94	11.53 ± 1.88	0.29	NS	14.25 ± 4.48	11.24 ± 0.70	0.70	NS
Chemical, moisture and total ash contents								
Calcium (%)	0.66 ± 0.11	0.75 ± 0.06	-0.76	NS	0.61 ± 0.12	0.76 ± 0.06	-1.19	NS
Chloride (%)	0.75 ± 0.03	0.71 ± 0.09	0.17	NS	0.99 ± 0.38	0.64 ± 0.08	1.42	NS
Copper (ppm)	5.17 ± 0.48	6.18 ± 0.61	-0.96	NS	5.49 ± 0.49	6.03 ± 0.59	-0.49	NS
Iron (ppm)	148.40 ± 36.20	117.00 ± 14.70	0.96	NS	174.23 ± 40.07	110.73 ± 14.08	1.89	NS
Magnesium (%)	0.20 ± 0.03	0.25 ± 0.02	-1.35	NS	0.19 ± 0.04	0.25 ± 0.02	-1.45	NS
Manganese (ppm)	46.12 ± 6.89	71 ± 94	-1.62	NS	61.55 ± 10.50	66.05 ± 8.75	-0.26	NS
Nitrate (ppm)	33.18 ± 9.10	27.14 ± 1.34	1.02	NS	38.42 ± 10.27	25.82 ± 1.32	2.07	P<0.05
Nitrogen (%)	1.10 ± 0.09	1.17 ± 0.07	-0.54	NS	1.16 ± 0.12	1.15 ± 0.07	0.09	NS
Phosphorus (%)	0.04 ± 0.00	0.05 ± 0.01	-0.88	NS	0.05 ± 0.01	0.05 ± 0.01	0.25	NS
Potassium (%)	0.58 ± 0.09	0.55 ± 0.09	0.22	NS	0.63 ± 0.10	0.53 ± 0.06	0.82	NS
Sodium (%)	0.31 ± 0.10	0.25 ± 0.03	0.17	NS	0.34 ± 0.11	0.25 ± 0.03	1.15	NS
Sulphur (%)	0.19 ± 0.02	0.24 ± 0.02	-1.23	NS	0.21 ± 0.02	0.24 ± 0.02	-0.72	NS
Zinc (ppm)	30.73 ± 5.30	43.72 ± 8.78	-0.87	NS	40.89 ± 6.06	40.04 ± 8.40	0.05	NS
Moisture Content (%)	52.25 ± 2.60	55.83 ± 1.55	1.17	NS	51.86 ± 3.18	55.72 ± 1.46	1.18	NS
Ash Content (%)	3.75 ± 0.73	4.60 ± 0.43	-0.98	NS	3.58 ± 0.87	4.60 ± 0.41	1.11	NS

Table 5 (continued)

Characteristic	Black-gloved wallaby				Western grey kangaroo			
	Chosen	Avoided	t or χ^2	Sig. Diff.	Chosen	Avoided	t or χ^2	Sig. Diff.
Morphological features								
Apex Type	—	—	12.08	NS	—	—	12.57	NS
Apex soft or hard	—	—	0.51	NS	—	—	0.79	NS
Glands present or absent	—	—	1.31	NS	—	—	6.55	P<0.05
Consistency	—	—	5.22	NS	—	—	6.60	NS
Adaxial tomentosity	—	—	2.30	NS	—	—	2.54	NS
Abaxial tomentosity	—	—	2.64	NS	—	—	5.30	NS

The morphological features of the plants selected and avoided by the two macropods were not generally different (Table 5). The type of leaf apex, whether the apex was soft or hard, the presence or absence of glands, leaf consistency, and adaxial and abaxial tomentosity, had no relationship to the types of plants consumed by black-gloved wallabies. Western grey kangaroos, however, avoided plants with leaf glands, notably the Myrtaceae. Other morphological characteristics had no relationship to the choices made by the western grey kangaroos.

Discussion

Central to the study of animal ecology is the use a herbivore makes of its environment, specifically the types of plants it consumes in the different habitats it occupies. It is not only worthwhile knowing what a herbivore eats, but also when and how much is consumed, the availability of the resource and the nutritional value of the plant to the animal (Free *et al.* 1970). It is also advantageous to understand the relationship between a herbivore and other species with which it co-exists, particularly the level of competition for shared resources. When shared resources are in limited supply, competition will eventually lead to the more successful competitor excluding the other. Management of animal populations in restricted range habitats, therefore, requires a wide array of information.

In this study, the black-gloved wallabies of Whiteman Park consumed a wide range of species, generally in moderate or small amounts rather than a few species in large amounts. However, *Carpobrotus edulis*, *Cynodon dactylon*, and *Nuytsia floribunda* were found in abundant amounts in the faeces. The succulent *Carpobrotus edulis* and the lawn *Cynodon dactylon* were the most abundantly consumed species in the drier seasons, a time when free-standing water was not readily available in the study area. The hemi-parasitic *Nuytsia floribunda*, the only species noted as abundant in the faecal samples of winter samples, might also be a likely source of moisture due to its ability to absorb water from neighbouring plants. The black-gloved wallaby has been noted by Christensen (1983) to be able to survive without free water. The Whiteman Park population of black-gloved wallabies would be especially well served with these moisture-rich plants for their source of water.

The western grey kangaroos of Whiteman Park showed a similar tendency as black-gloved wallabies to consume a wide variety of plant species in limited amounts. As for black-gloved wallabies, these larger

marsupials consumed abundant quantities of the exotic, succulent *Carpobrotus edulis* and the lawn grass *Cynodon dactylon* among the 25 dietary plant species. As in previous studies (Halford *et al.* 1984b; Shepherd *et al.* 1997), it appears that the western grey kangaroo is a versatile feeder, consuming a wide variety of plant species and plant types.

Consumption of a wide variety of plant species is seen both as an adaptation to the prevention of adverse effects from plant poisons (Howe & Westley 1988), but also a necessity, as the plant species of Whiteman Park have very low cover percentages. A mixed species diet is therefore required to provide sufficient energy for survival. Limited grazing and browsing on a range of plant species is also of significance to the management of Whiteman Park, as herbivore pressure on any individual plant species is not likely to result in local extinction.

Hume's (1982) review of marsupial nutritional requirements concludes that potoroid and small macropod species generally ingest plants of higher nutritive value than do larger (greater than 10 kg) macropods. A relationship between body size and nutritive value of preferred diets has also been reported for eutherian herbivores (Demment & Van Soest 1985). Total energy requirement of animals tends to increase with increasing body mass, but at a progressively slow rate. Thus, although larger animals require more total energy (kJ d^{-1}), small animals require more energy relative to body mass ($\text{kJ kg}^{-1} \text{d}^{-1}$) (Freudenberger *et al.* 1989). It may be that subtle differences in food perception are responsible for the observed differences in selection. A smaller animal may be capable of distinguishing food types on a finer scale than larger animals (Norbury & Sanson 1992). In this study, however, the measured chemical constituents and the range of morphological features described for leaves between chosen and avoided species were not different. It is believed that different plants within a plant community have varying palatabilities for grazing sheep (Krueger *et al.* 1974). Although taste is of primary importance in diet selection in sheep, smell, sight and touch also play a role, although they may be of minor importance. Unfortunately, such information is not known for the majority of herbivores, including macropods. Until it is known whether senses such as taste, smell, sight and touch significantly affect a macropod's food perception, and if so to what extent, problems will remain as to whether measured food availability is the same as perceived food availability.

Halford *et al.* (1984b) showed that plants potentially high in nitrogen (*i.e.* legume species) were preferentially

browsed by western grey kangaroos in a *Eucalyptus wandoo*-grass pasture landscape near Bakers Hill. The results in the present study indicated that nitrate levels of selected species was higher than avoided species. Although an ability to select plant species of high nitrate condition or high protein level would be a valuable asset for the herbivore, we feel this finding should be viewed with caution for a number of reasons. Firstly, it is doubtful that western grey kangaroos would not obtain enough nitrogen in their normal diet and, therefore, seek out plants high in nitrates. Even if they did, kangaroos would need the appropriate microbial symbionts in their digestive systems to convert the nitrates to nitrites, so they could be assimilated. We are not aware if this species has such microbial symbionts. Secondly, it is also doubtful if these kangaroos can perceive parts per million concentration differences in leaf content of nitrates. Thirdly, due to the number of comparisons analysed, it could be expected that one comparison might be falsely indicated as different. Further detailed comparisons would be necessary to confirm the ability of this marsupial herbivore to select high nitrate containing plants.

Western grey kangaroos appear to avoid plant species with oil glands. Black-gloved wallabies, on the other hand, consumed a number of species with oil glands, but only in small or moderate amounts. The evolutionary significance of oil glands in the Myrtaceae and Rutaceae families is uncertain, but it is possible that they play a role in the prevention of herbivory. However, the detection of diet selection by herbivores is a very complicated task. Many factors must be considered, such as positive nutritional elements, negative compounds, such as lignin, tannins, pectins and toxin, water requirements and morphological characteristics of leaves, stems and branches. Considering each of these factors separately can give clues to diet selection, but an ideal method of analysis would simultaneously take all factors into consideration for each plant species. For example, a plant species may have high positive nutrients and high water content, but the present of pungent spines or toxins may render the plant inedible for certain herbivore species. Searching for trends in the light of specific characters may, therefore, be an oversimplified and inappropriate method of determining diet selection. Although the use of more sophisticated multivariate statistical techniques might lend further knowledge on diet selection, the characters are not independent of one another, and therefore, this statistical technique is invalid on mathematical grounds.

This study of dietary preference in black-gloved wallabies and western grey kangaroos in Whiteman Park has confirmed their polyphagous nature. The diversity of plant species in Whiteman Park provides a wide range of dietary choices for both herbivores. Competitive exclusion is not considered to be cause for concern as the vegetation of Whiteman Park provides a large number of acceptable food resources for both animals. The provision of significant numbers of high moisture content plants would favour the continued survival of both species, but especially the black-gloved wallabies that require plant-derived moisture rather than free-water sources.

Acknowledgments: We are grateful for cooperation throughout the study to A Brian, H Gratte and R Wagland of the Whiteman Park Staff and K A Shepherd of the Department of Botany, University of Western Australia.

Funds for the research were provided through the Department of Botany Teaching and Research Block Grants.

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Waychinicup Estuary, Western Australia: the influence of freshwater inputs on the benthic flora and fauna

J Phillips & P Lavery

Department of Environmental Management, Edith Cowan University, Joondalup WA 6027:
email p.lavery@cowan.edu.au

Received October 1996, accepted March 1997

Abstract

Waychinicup Estuary (south-western Australia) is dominated by tidal and swell exchange with the ocean and receives seasonal, but low, freshwater inflows. The estuary was surveyed in September 1995 to determine the significance of freshwater inflows to its ecology and to provide a detailed inventory of benthic flora and fauna because, like other estuaries, Waychinicup may come under pressure for diversion of inflows to meet demand for potable water.

Gradients detected in benthic flora and fauna, sediment grain size and organic content, and water quality, were related to distance from the river mouth. Sediments closest to the river mouth had a higher organic content and a higher percentage of $<63 \mu\text{m}$ particles. These areas had a low water clarity (SDD = 0.6m). Further from the river, the sediments became less organic and coarser, and water clarity increased (SDD >7 m). We hypothesise that biotic gradients in the estuary are determined by freshwater inflow, principally through its contribution of fine and organic sediments, and less so through its effect on salinity. These sediments are prone to resuspension, reducing water clarity, limiting plant growth and providing a niche for euryhaline, low light-adapted macroalgae and a polychaete-dominated infauna in the upper estuary. Change in sediment type, increase in water clarity and increasing salinity produces a shift to a diverse macroalgal and seagrass community, and an amphipod-dominated benthic fauna in the lower estuary.

Despite the dominance of oceanic exchange in the estuary, freshwater inflow is a key determinant of the composition and distribution of biota. Any significant reduction in freshwater inflow is likely to cause a change in water quality and biota; the system would have lower organic inputs, become clearer, and the plant and animal assemblages currently found in the upper reaches of the estuary may well be lost.

Introduction

The south coast of Western Australia has a diverse array of estuaries and coastal lagoons, ranging from those permanently open to the ocean through to some which are permanently closed. Cumulatively, as well as individually, these systems have enormous ecological, scientific and educational value. Like many ecosystems, however, these estuaries and coastal lagoons face potential threats. Among the most serious of these is the increasing demand for potable water supplies that accompanies recreational activities and tourism developments adjacent to estuaries. One means of meeting this demand is damming of the small rivers which feed the estuaries, and most at risk are those estuaries with relatively pristine catchments and reliable flows of freshwater.

Estuaries are characterised by highly variable ecological conditions due to the mixing of marine and fresh water. The stress this places on estuarine biota is a major determinant of the biotic community structure and leads to gradients in both floral species diversity (Doty & Newhouse 1954; Munda 1978; Josselyn & West 1985; Montague & Ley 1993) and faunal species diversity (Jones *et al.* 1986; Montagna & Kalke 1992) related to salinity gradients. Changes to the freshwater inflow regime may alter the complex biophysical relationships and are

likely to have significant implications for estuarine biotic distribution.

While Waychinicup Estuary is not at all typical of other estuaries in the region, it does typify those estuaries most at risk of disturbance due to the future demand for freshwater. It is located close to significant demands for freshwater (the major urban centre of Albany is only 44 km to the west while nearby Cheyne Beach and the Two Peoples Bay Nature Reserve are increasingly used by tourists who require freshwater). Coupled with this, Waychinicup Estuary has a relatively reliable streamflow of potable water from a largely undisturbed catchment.

The role of freshwater inflow into Waychinicup Estuary was examined in relation to the benthic flora and fauna, and water quality parameters. The estuary itself is only about 1300 m in length and over half of this length is less than 2 metres deep. The system is well flushed by tidal and swell action and riverine input is small in comparison to the degree of oceanic exchange. Thus, it might be easy to dismiss the significance of relatively small inputs of freshwater as a determinant of biotic composition. However, we show that freshwater inputs are significant in this regard, but not through the simple effect of salinity variation.

A further objective of the study was to provide a baseline inventory of benthic biota in the estuary. The highly marine nature of this estuary also suggests that

the benthic flora within the estuary may serve as a useful indicator of benthic flora in adjacent marine areas. Despite increasing threats to the estuaries of the south-west, there is a noticeable absence of comprehensive baseline data, apart from the preliminary inventories by Hodgkin & Clark (1988a,b, 1989a,b, 1990a,b).

Methods

Study area

Waychinicup estuary is located on the southern coast of Western Australia ($34^{\circ} 54' S$ $118^{\circ} 19' E$; Fig 1), approximately 44 km east of Albany. The area has warm summers and cool winters, and receives approximately 750 mm rainfall per annum.

The estuary is unique in the region. It is the only estuary with steep rock shores along most of its 1300 m length. Rocky headlands maintain a wide opening to the ocean, allowing relatively undampened influences of oceanic swells and tides and maintaining permanent exchange with the ocean. The Waychinicup River, the estuary's only riverine source, has a catchment of 145 km² of which 41% has been cleared (Hodgkin & Clark 1990b). The lower valley of the Waychinicup River and the Waychinicup Estuary are both within the Waychinicup National Park.

Data were collected on two visits to the estuary, on 2 September and 18 September 1995. Biotic and physico-chemical variables were examined on each occasion.

River flow

Total monthly stream records for the period 1970-1995 were obtained for the Waychinicup River Gauging Weir (# 602031) from the Water and Rivers Commission of Western Australia. These data were analysed to provide total monthly, winter and annual stream flow volumes and long-term average winter and annual flow volumes.

Macroalgae and seagrass

Nine transects were established at intervals along the length of the estuary as well as individual quadrat samples at the head of the estuary where the narrowness of the estuary did not allow transects (Fig 1A). The cover and composition of macroalgae and seagrass were recorded in quadrats (0.25 m²) at 10 m intervals along the transect. Where transects occurred on areas of rocky granite and steep sides, quadrats were also taken at depth intervals. Data on seagrass distribution was supplemented by spot dives. All samples were identified to the lowest taxonomic level possible using keys of Huisman & Walker (1990) and Womersley (1984, 1987, 1994).

Patterns in macroflora assemblages were examined using the multivariate statistical analysis package PATN (Belbin 1993). All analyses were based on a presence/absence data matrix recorded for each quadrat using non-hierarchical allocation (Belbin 1987). Allocation was conducted following a Bray & Curtis association measure. This was selected as a dissimilarity measure since it is the most accepted measure used for ecological data (Faith *et al.* 1987). A radius of 0.6 was selected to define groupings in the allocation.

Benthic invertebrates and infauna

The presence and abundance of benthic invertebrate fauna was determined along three transects (Fig 1A).

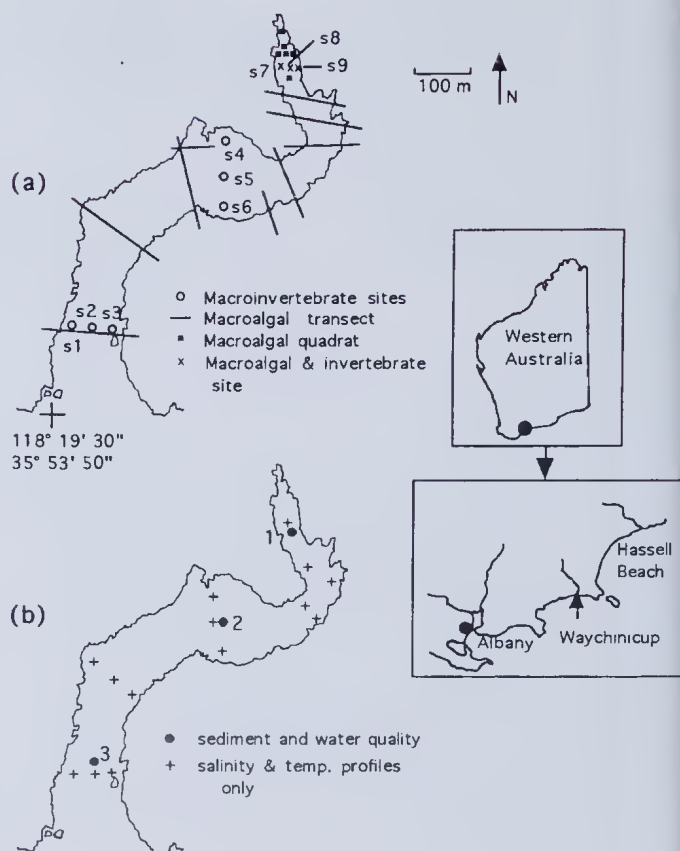


Figure 1. Sampling site locations for (A) benthic flora and macroinvertebrates and (B) sediments and water quality profiles in Waychinicup Estuary.

Three replicate core samples (120 mm diameter and 10 cm deep) were randomly taken from within the first, central and last 0.25 m of the transect. Core samples were sieved (1.0 mm) on location and preserved with buffered seawater formalin solution.

Material retained on the sieve was flooded in a tray to sort for invertebrates. One observer spent 15 minutes picking out any visible invertebrates from each sample. Then, a second observer spent five minutes on the same sample to check for any overlooked organisms. This standardised processing was intended to reduce observer bias and to impose a common effort on each sample. Invertebrates were identified to the lowest taxonomic level possible using Brusca & Brusca (1990), Wells & Bryce (1984, 1988), Hutchings (1984) and Shepherd & Thomas (1982, 1984).

PATN was used to explore patterns in infauna assemblages, based on a species abundance data matrix recorded for each replicate (core). Classification of the replicates following the Bray & Curtis association was conducted by flexible UPGMA, using a beta value of zero. Species groupings were determined by a two-step association measure prior to a flexible UPGMA. Quadrats were also ordinated in two dimensions following Bray & Curtis association, using non-metric multidimensional scaling.

Sediment sampling

Sediment grain size and organic content were sampled at three sites on a longitudinal transect in the centre of

the estuary (Fig 1B). At each site, three replicate sediment cores were collected to a depth of 2 cm using 50 mm perspex corers.

Sediments were weighed then dried for 82 hours at 75 °C. Organic content was determined by combusting samples for two hours at 550 °C. Samples were then re-wet with deionised water and allowed to stand for two hours before wet-sieving through a 63 µm sieve. Water and sediment passing through the sieve were transferred into 10 mm centrifuge tubes and centrifuged for 15 minutes at 1800 rpm. The supernatant was removed and the remaining pellet of sediment was placed into a crucible and dried at 75 °C to determine the dry weight of the <63 µm fraction.

A subsample of each <63 µm sediment sample was combusted for one hour at 950 °C to determine the calcium carbonate (CaCO_3) content. Complete burn-off of CaCO_3 was verified by calculating the reduction in mass of CaCO_3 standards combusted with the samples. The CaCO_3 mass was used as an indication of fine particulate origin, with low content being interpreted as indicating a greater likelihood of terrigenous origin.

The mean proportion of organic matter and <63 µm fraction recorded for each site was compared by analysis of variance (ANOVA). Separate one-way ANOVAs were conducted for each, using arcsine-transformed data, followed by Fisher's PLSD pairwise comparisons (Zar 1984).

Water quality

Horizontal and vertical salinity profiles were recorded along the length and width of the estuary (Fig 1B), using a Yeo-kal Hamon Salinity-Temperature Bridge (MKII Model 602). Surface and bottom readings for temperature and dissolved oxygen (DO) were taken using a Yeo-kal Dissolved Oxygen/Temperature Model 630 meter. Light penetration was recorded using a Secchi disc.

Surface and bottom water samples were collected during each visit to the estuary, at three sites (Fig 1b). Bottom water samples were taken using a vanDorn bottle. Filtered (GFC 0.45 µm) samples were analysed for nitrate and nitrite, ammonia and orthophosphate using a Hach DR 2000 spectrophotometer, as per the cadmium reduction, salicylate, and ascorbic acid methods respectively (Anon 1989).

Results

Stream flow

Monthly, winter and annual streamflow for Waychinicup River are shown in Fig 2. Monthly flow was highly variable with the majority of flow occurring in the winter (June-September) period. Average annual flow (1970-1995) was $9.15 \times 10^6 \text{ m}^3$, while the average winter flow over the same period was $6.02 \times 10^6 \text{ m}^3$. The recorded winter flow in 1995 was $1.88 \times 10^6 \text{ m}^3$, or only 31 % of the long-term average winter flow volume and the third lowest flow on record. However, interannual variation was high and the long-term average was greatly enhanced by the high flows in 1978 and 1979. Eleven years (44 % of recorded winters) had flows of less than $3 \times 10^6 \text{ m}^3$ indicating that low flow years are not rare. The following results are probably indicative of the lower flow years.

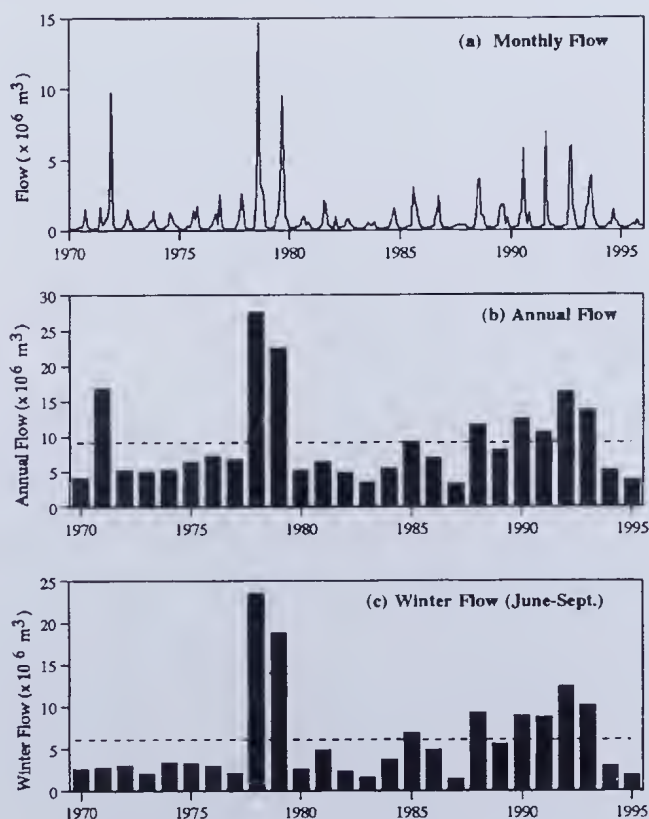


Figure 2. River flows for the Waychinicup River, 1970-1995. Dashed lines indicate the 1970-1995 average.

Physico-chemical variation

All of the measured variables showed detectable changes clearly associated with increasing distance from the river mouth.

There were both vertical and horizontal variations in salinity through the estuary with surface salinities consistently lower than bottom salinities (Fig 3). In September, stratification was greatest at the river mouth and least at 350 m from the river mouth where water depth was only 1.25 m. Surface salinity varied from 21.6 ppt at the head of the estuary to 33.9 ppt at the seaward mouth (Fig 3). Bottom salinity readings showed a smaller range of variation, from 27.4 ppt at the head of the estuary to 35.6 ppt in the lower reaches.

Surface temperatures ranged from 14.7 °C at near the river mouth to 16 °C at 810 m and 1070 m from the river mouth respectively (Fig 3). Similarly, bottom temperature readings increased from 14.9 °C at site 1 to 16.2 °C at site 13. Temperature stratification was evident throughout the estuary, though only marginally so at 400 m from the river mouth.

Oxygen concentrations were consistently high throughout the estuary (Table 1; corresponding saturation values ranged between 94 - 102 %) with only minor spatial differences.

Variations in the concentrations of dissolved inorganic nitrogen (ammonia, nitrate+nitrite) and phosphorus (orthophosphate) were similar on both sampling dates, and so only data for 18/9/95 are shown in Table 1. Only orthophosphate showed a clear spatial variation, with very high concentrations near the river mouth and low

concentrations elsewhere. The concentration of inorganic nitrogen varied negligibly through the estuary. There was noticeable stratification of orthophosphate in the upper reaches of the estuary (site 1) with the upper, less saline layer having almost four times the concentrations of the bottom waters. Corresponding to the variation in orthophosphate concentrations was a gradient in N:P ratios of the water column. The upper and middle estuary had ratios less than 16:1 and so could be classified as potentially N limited waters. It must be emphasised that these values are for a single sampling occasion at a time of low flow.

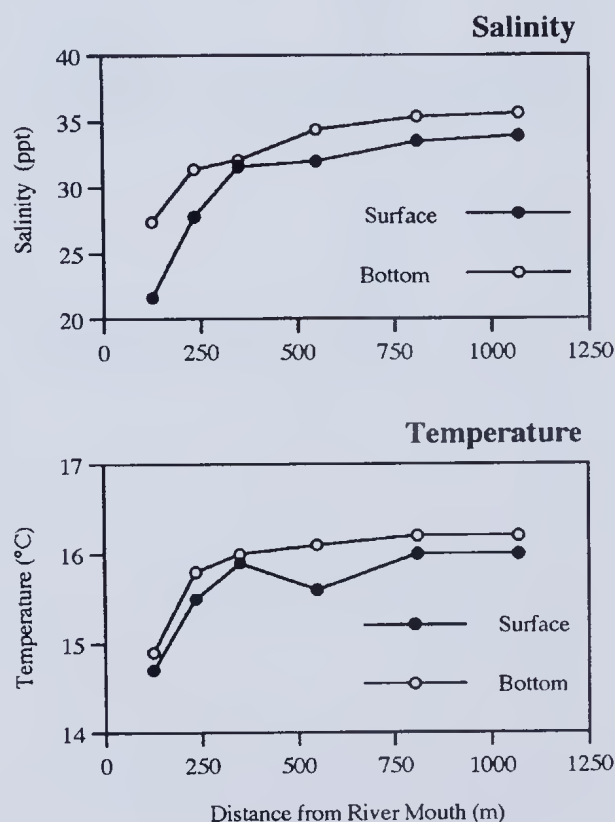


Figure 3. Water column salinity (top) and temperature (bottom) for surface and bottom water in Waychinicup Estuary, September 1995.

Table 1

Nutrient concentrations in Waychinicup Estuary on 18 September 1995. N:P ratio is for dissolved inorganic ions.

NUTRIENT		Site 1	Site 2	Site 3
PO ₄ -P (mg L ⁻¹)	Surface	0.11	0.00	0.01
	Bottom	0.03	0.02	0.02
NO ₃ -N (mg L ⁻¹)	Surface	0.07	0.08	0.07
	Bottom	0.03	0.03	0.03
NH ₃ -N (mg L ⁻¹)	Surface	0.00	0.00	0.01
	Bottom	0.00	0.00	0.00
N:P Ratio	Surface	0.6	16	8
	Bottom	1.0	1.5	1.5
O ₂ (mg L ⁻¹)	Surface	8.2	7.0	8.2
	Bottom	8.7	7.3	8.3

Sediments and light attenuation

As with the water column parameters, the sediment characteristics showed a clear gradient corresponding to distance from the river mouth. Mean organic matter content decreased with increasing distance from the river mouth (Table 2). The variation between sites was significant (ANOVA, $P < 0.05$; data arc-sine transformed). Site 1 had a significantly higher percentage organic matter than site 2 ($P = 0.02$, Fisher's PLSD) and site 3 ($P < 0.01$), but sites 2 and 3 were not significantly different. The greatest variation was observed at site 2, which supported a seagrass meadow.

Table 2

Mean ($\pm$ standard deviation, $n = 3$) of sediment characteristics, Secchi disc depth and water depth in Waychinicup Estuary. Sites 1, 2 and 3 were 125 m, 550 m and 1070 m from the river mouth respectively. Sediment data are the transformed values derived from percentage by weight data.

Parameter	Site 1	Site 2	Site 3
Organic matter (%)	13.4 $\pm$ 0.8	9.3 $\pm$ 2.5	7.8 $\pm$ 0.6
Grain size <63 μ m (%)	18.0 $\pm$ 0.7	14.8 $\pm$ 2.9	12.1 $\pm$ 0.4
Secchi disc depth (m)	0.65	1.4	7.5
Water depth (m)	1.6	2.0	9.2

The above trends were also reflected in fine particle fraction (Table 2). Site 1, closest to the river mouth, had the highest fine particle fraction. The variation between sites was statistically significant (ANOVA, $P < 0.05$). Fisher's PLSD indicated significant differences between sites 1 and 3 ($P < 0.01$). The greatest variation was again observed at site 2, which supported a benthic seagrass community.

Secchi disc depths increased with increasing distance from the mouth of the river (Table 2) thus varying positively with temperature and sediment organic content and fine particulate fraction. Secchi disc depth in the upper estuary was 0.65 m or 40% of the water column depth. In contrast SDD was over 7.5 m or 80% of the water depth at the lower site.

Benthic flora

There were clear spatial patterns in the benthic plant assemblages through the estuary which again coincided with increasing distance from the river mouth and the gradient in physico-chemical parameters.

Forty species of macroalgae and five species of seagrasses were recorded in the estuary (Table 3). Fourteen groups of benthic flora were identified, falling into two broad categories; those on the estuary floor or those on the vertical rock walls. The distribution of 'estuary floor' groups showed a strong gradient of species change in the upper reaches of the estuary (Fig 4). Fine green and red algae were limited to the upper 80 m of the estuary, whilst a mixed algal assemblage dominated by *Cystoseira trinodis* was restricted to an area of hard substratum between 150 m and 300 m from the river mouth. Elsewhere, the substratum was muddy to sandy and supported seagrasses (Fig 4). The seagrasses *Posidonia australis* and *Heterozostera tasmanica* were widespread although their distribution was generally limited to areas further

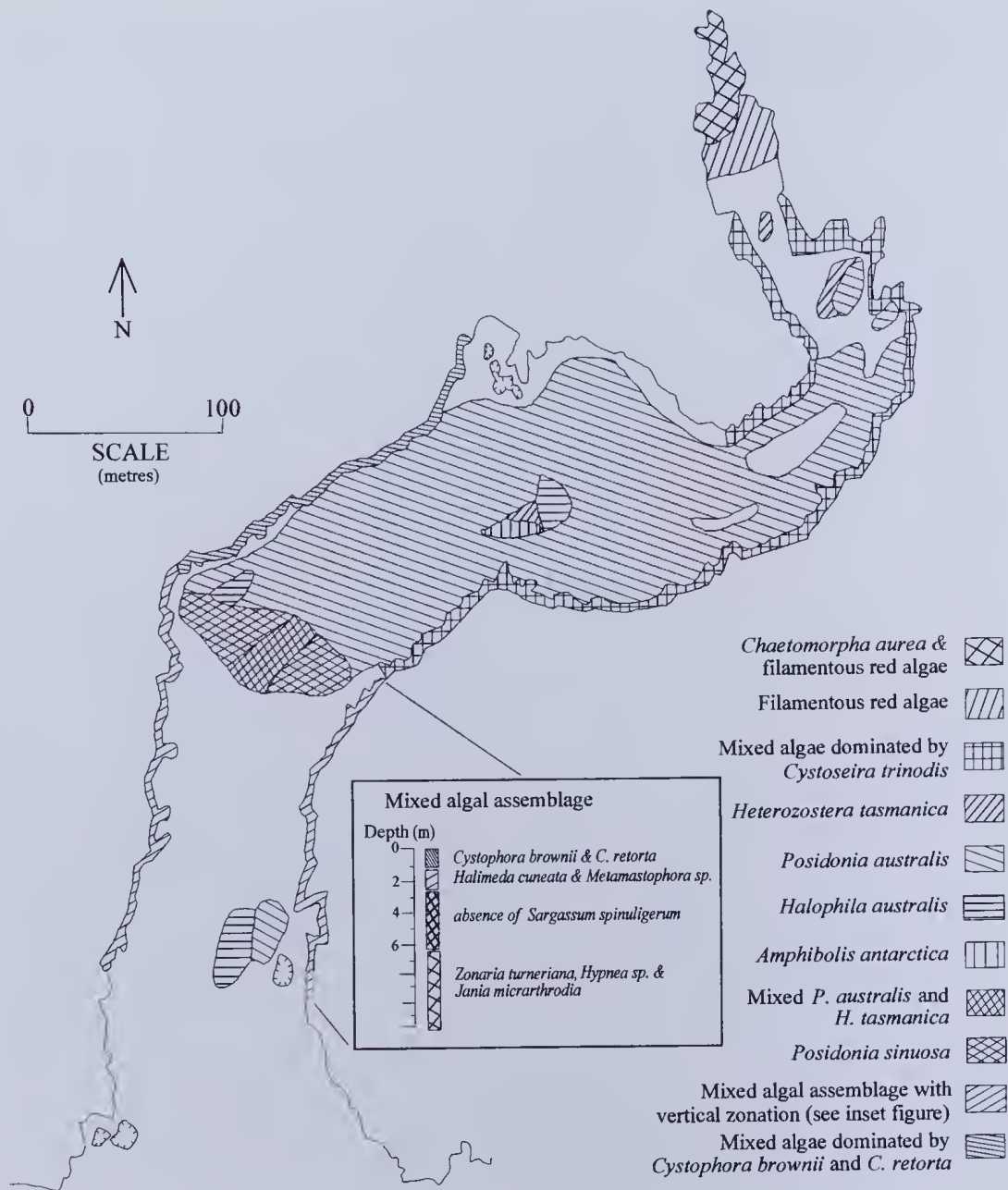


Figure 4. Distribution of benthic flora assemblages in Waychinicup Estuary, September 1995.

than 200 m from the river mouth. *Posidonia sinuosa*, a seagrass that is usually found in higher energy environments, was found only near the mouth of the estuary. Three other species, *Halophila australis*, *Heterozostera tasmanica* and *Amphibolis antarctica* occurred in small patches throughout the estuary.

The vertical rock faces in the lower reaches of the estuary supported a mixed algal assemblage dominated by brown and red algae. Allocation analysis indicated vertical zonation (Fig 4).

Benthic invertebrate and infauna assemblages

The two-dimensional ordination from pooled replicate data showed patterns in sites relating to location within the estuary (Fig 5). There were three clear groups, with

all sites for each of the the upper, middle and lower estuary transects clustering together. The dendrogram from classification of all replicate data from the nine sites also reflected this pattern with the upper estuary sites (1, 2 & 3; 150 m from the river mouth) showing a high dissimilarity to other sites. A cut-off value of 0.96 (a very high degree of dissimilarity) produced five groups of sites with the three upper estuary sites clearly separating out as one group (Fig 5).

There was a shift from small crustacean dominated sites at the mouth of the estuary to sites dominated by polychaete worms in the upper reaches of the estuary (Table 4). The pattern of species shift shown by the classification and ordination analyses (Fig 5) corresponded well to the dominant sediment type at each site (Table 5).

Table 3

Benthic macrophyte species recorded in Waychinicup Estuary (September 1995) and their approximate distances from the river mouth.
* indicates presence.

	metres from river mouth														
	5	30	60	80	100	120	160	210	270	360	510	610	650	810	1070
<i>Chaetomorpha aurea</i>	*		*	*											
filamentous red sp 1		*		*	*										
<i>Heterozostera tasmanica</i>						*	*	*	*	*				*	
<i>Cystoseira trinodis</i>							*	*	*	*	*		*	*	
filamentous red sp 2							*	*	*	*	*				
<i>Sargassum spinuligerum</i>							*	*	*	*				*	*
<i>Posidonia australis</i>							*	*	*	*	*	*	*	*	*
<i>Colpomenia sinuosa</i>								*		*					
<i>Laurencia</i> sp 1								*		*				*	*
<i>Phloiocaulon spectabile</i>											*	*			
<i>Cystophora brownii</i>												*	*	*	*
<i>Cystophora retorta</i>												*	*	*	*
encrusting red coralline sp 1												*	*		*
encrusting red coralline sp 2												*	*	*	*
<i>Hormosira banksii</i>													*	*	
<i>Posidonia sinuosa</i>														*	
<i>Amphibolis antarctica</i>														*	
<i>Dictyopteris</i> sp														*	
<i>Chondria</i> sp														*	
<i>Laurencia</i> sp 2														*	
<i>Metagoniolithon radiatum</i>														*	*
<i>Halophila australis</i>														*	*
<i>Ecklonia radiata</i>														*	*
<i>Lobophora variegata</i>														*	*
<i>Sargassum distichum</i>														*	*
<i>Halptilon roseum</i>														*	*
<i>Sargassum</i> sp 1															*
<i>Dictyosphaeria sericea</i>															*
<i>Cystophora</i> sp															*
<i>Caulerpa distichophylla</i>															*
<i>Amphiroa anceps</i>															*
<i>Halimeda cuneata</i>															*
<i>Phacelocarpus adopus</i>															*
<i>Metamastophora</i> sp															*
<i>Zonaria turneriana</i>															*
filamentous red sp 3															*
<i>Dictyota dichotoma</i>															*
<i>Hypnea</i> sp															*
<i>Sargassum</i> sp 2															*
<i>Sargassum tristichum</i>															*
<i>Cystophora monilifera</i>															*
<i>Jania micrarthrodia</i>															*
<i>Rhipiliopsis peltata</i>															*
<i>Lenormandia spectabilis</i>															*
<i>Stenogramme leptophylla</i>															*

Discussion

The unique physical and hydrologic features of Waychinicup Estuary, which have been described above, are clearly reflected in its benthic flora. With over forty five species, Waychinicup Estuary has an exceptionally rich benthic flora. By comparison, the vast majority of other south coast estuaries are dominated by three species of benthic macrophyte, *Ruppia megacarpa*, *Polyphysa peniculus* and *Lamprothamnion papulosum* with its associated epiphytes (e.g. Hodgkin & Clarke 1989a,b, 1990).

The benthic flora of Waychinicup Estuary is predominantly a marine intrusion flora. The seagrasses in the system are typical of coastal marine areas not estuaries, and the macroalgal assemblages in the lower reaches are dominated by species typical of southern Australian marine flora (Womersley 1984, 1987, 1994). In this respect, the algal composition of the lower reaches recorded in this winter survey is likely to be a better representation of open coastal marine flora of the south coast than it is of other estuaries.

Table 4

Benthic macroinvertebrates recorded in Waychinicup Estuary (September 1995) and their approximate distances from the river mouth. (See Fig 1A for site locations). p = Polychaetae, mx = Maxillopoda, m = Malacostrata, g = Gastropoda, s = Sipunculada, o = Oligochaetae, b = Bivalva. 1 is < 250 m², 2 is < 500 m², 3 is < 800 m², and 4 is > 800 m².

	Region: Lower			Middle			Upper		
	Site: 1	2	3	4	5	6	7	8	9
<i>Lyssianassidae</i> sp (m)	2								
<i>Spio pacifica</i> (p)	4	4	1				1	1	
maldanid sp 1 (p)	1	1							
<i>Odontosyllis</i> sp (p)	1	1	1	1	1				
<i>Birubius</i> sp (m)	1	1	1						
<i>Paphies</i> sp (b)	1		1	1			1		1
<i>Tipimegus</i> sp (m)	1		1	1					
<i>Anthuridae</i> sp (m)		1							
mysid sp 1 (m)		1							
<i>Aricidea fauveli</i> (p)		1	1		1	1			
<i>Phallodrilus wellsi</i> (o)		1	1			1			
amphipod sp (m)			1						
<i>Austropeonoides</i> sp (m)			1						
<i>Oedicerotidae</i> sp (m)			1						
<i>Paradexamine</i> sp (m)			1						
ostracod sp 1 (mx)			1						
<i>Rhinothelepus setosus</i> (p)			1	1					
<i>Guerneia endota</i> (m)			2	1					
<i>Golfingia</i> sp (s)			1		2	1	1		
<i>Leonnates</i> sp (p)				1					
oligochaete sp (o)				1				1	
<i>Bititium</i> sp 1 (g)				3					
<i>Bititium</i> sp 2 (g)				1					
<i>Spisula trigonella</i> (b)				1		1	1		
<i>Paratanais ignatus</i> (m)				1		1	1		
<i>Apseudidae</i> sp (m)				1	1	1	1		
<i>Caullierella</i> sp (p)					2	1			
<i>Capitella capitata</i> (p)						1	2	4	1
maldanid sp 2 (p)					1				
<i>Notomastus estuarius</i> (p)					1		1		
<i>Naineris grubei</i> (p)					1		1	1	1
<i>Leitoscoloplos bifurcatus</i> (p)						1			1
<i>Katyelsia rhytiphora</i> (b)						1			
<i>Tethygeneia nalgo</i> (m)						1			
mysid sp 2 (m)									1
Total Species		19			23			12	

Notwithstanding the above, our results clearly indicate that other factors are important in shaping the distribution patterns in the upper reaches of the estuary. Salinity may be an important determinant of macroalgal distribution in Waychinicup Estuary, but in association with turbidity. Only two algal assemblages penetrated to the very head of the estuary. This trend of reduced diversity in the upper reaches of estuaries is often ascribed to salinity effects (McLusky 1989; Morrissey 1995) though in this case it appears to be a combination of both salinity and light attenuation. The fine green alga in the upper reaches (*Chaetomorpha*) is typically adapted to variable salinity regimes and better adapted to poor light conditions than larger brown and red algae (Lavery 1989). Other macroalgal groups in the upper and mid-estuary reaches showed a strong gradient of species changes, which may be due to factors other than light penetration. Not only did benthic plant groups change along a gradient of increasing salinity, but vertical groups also changed with

increasing salinity. Although vertical species shift would be partly depth-related those groups that occurred at the water line must be able to tolerate, in addition to wave action, a relatively wide range of salinity given the freshwater lens that was evident at the time of this study.

All of our results suggest that freshwater inflow is a significant determinant of biological gradients in Waychinicup Estuary. This is despite the relatively small volume of inflow, its seasonality, and the degree of ocean exchange which is large. Thus while it might be argued that this system is in fact a simple river mouth with granite headlands, the parameters measured in this study clearly suggest it is, at least seasonally, a stratified estuary. In drawing this conclusion, it must be stressed that the estuary was surveyed over a limited period in one of the lowest flow years recorded. While the conditions in the estuary therefore represent a 'snapshot', they were probably a conservative estimate of the role freshwater inputs play in the system. It is probable that the role of freshwater in

Table 5

Qualitative description of sediment characteristics in Waychinicup Estuary.

Location	Site	Sediment type
lower reaches	1 - 3	coarse sand/shell fragments
middle reaches	4	medium to coarse sediments; some organic matter
	5	fine to medium sediments; some organic matter
	6	medium to coarse sediments; accumulation of dead shells
upper reaches	7	fine mud and sands with fine organics and seagrass detritus
	8	fine muds/silt
	9	seagrass detritus over medium coarse sediment and shells

driving biological gradients will be greater in higher flow years.

There was a gradient in most variables that related to distance from the source of riverine inflow, indicating that during these flow conditions freshwater inflows are affecting several variables, not just salinity. In particular, freshwater inflow appears to influence sediment distribution with subsequent effects on water clarity and sediment characteristics which directly affect benthic floral and faunal distributions.

Three possible sources of fine sediment within Waychinicup Estuary are the inflowing river, the coast, and from the margins of the estuarine basin itself (Carter, 1988). The margins were considered to contribute the smallest proportion of fine sediment, however, due to the large area of granite rock bordering the estuary. Fine sediments of marine origin in the form of calcium carbonate (from organisms such as foraminiferans and the weathering of shell material) were eliminated from samples taken from all three sediment sampling sites, leaving only clays and silicas. Since organic matter had been removed, it can be concluded that the remaining fine sediments were predominantly introduced with freshwater inflow, and this appears to be supported by the gradient of decreasing proportion of fine particles with increasing distance from the river source.

The gradient in sediment characteristics in Waychinicup Estuary provides a range of microhabitats for benthic invertebrates. Richness and abundance of benthic invertebrate species appeared to be related to differences in microhabitats and in particular sediment characteristics. Furthermore, invertebrate assemblages varied not only between transects but also within transects, suggesting that sediment characteristic gradients also existed across the estuary, most likely the result of seagrass distribution modifying the longitudinal gradient of sediment type.

The salinity stratification was correlated with higher levels of nutrients in surface waters in the upper reaches of the estuary. High levels of phosphate were expected, given that the upper catchment of Waychinicup River is

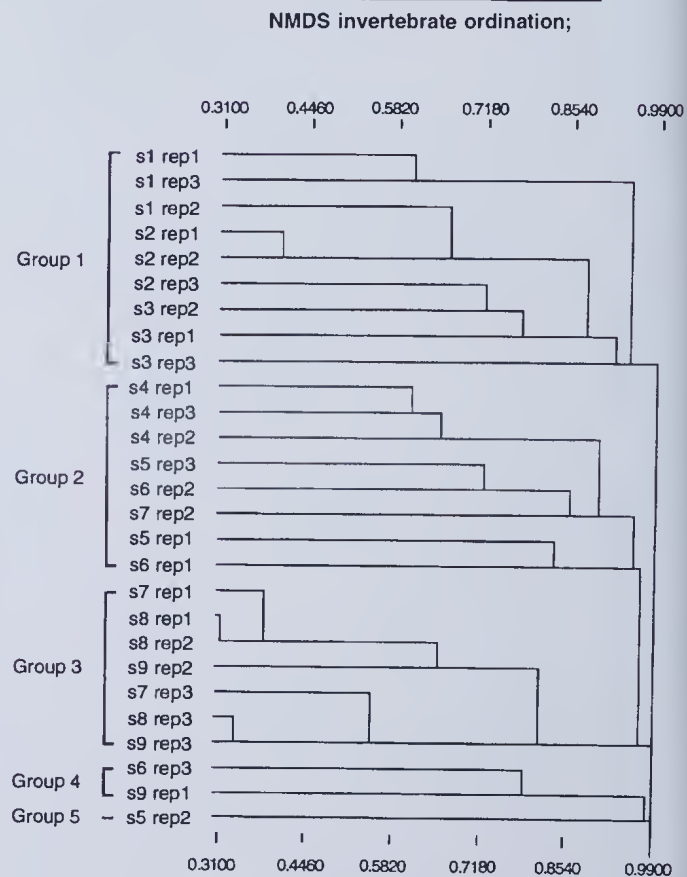
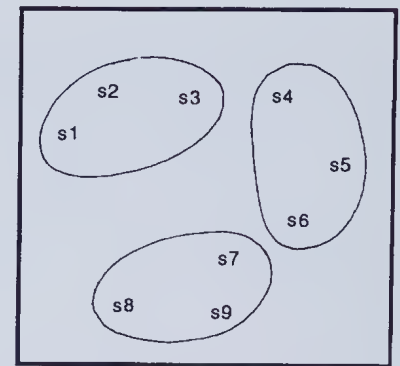


Figure 5. Ordination and associated dendrogram of sites and replicates based on the presence/absence of benthic macroinvertebrate fauna. See Fig 2 for site locations (s1 rep 1 = site 1 replicate number 1 etc).

cleared for agriculture, and this was indeed the case at the time of this study. The dissolved phosphate concentrations were comparable to those in highly eutrophic estuaries of south-western Australia (Lukatelich & McComb 1986). However, at the time of sampling a high degree of tidal exchange was evident as well as short term oscillations in the direction of flow due to incoming swells through the estuary mouth. Together with the degree of stratification, these exchange will significantly reduce nutrient accumulation, and the associated effects, within the estuary.

Management implications

It is clear that freshwater inflow into Waychinicup Estuary has a significant influence on the nature of the estuary. The results of the winter survey clearly emphasise the uniqueness of this estuary, and its ecological

and conservation value. Within this very small inlet/estuary there is a clear gradation from an 'estuarine' to open marine flora which is not recorded for any other system along the south coast. Any diversion of freshwater inflows to this system would therefore impact its ecology. It can be easy to overlook the importance of a small, seasonal freshwater input to an inlet which is so obviously dominated by tidal and oceanic swell exchange. Yet, any significant reduction in freshwater flow would reduce particulate loads to the estuary and, subsequently, sediment characteristics and the distribution and composition of benthic biota. While seagrasses might extend further up the estuary, the coarser sediments and lower turbidity would produce a more homogenous flora and possibly exclude the benthic invertebrate assemblages associated with fine mud and silt. Finally, reduction in freshwater inflow may reduce the degree of stratification and enhance vertical mixing in the estuary.

In conclusion, there are expected to be changes to the nature of the estuary in the event that freshwater is dammed or diverted, but how important such changes would be depends on how the estuary is valued. Given the estuary's location within Waychinicup National Park, it is assumed that it would be a management objective to preserve it for its intrinsic values, and so any alteration in the nature of the estuary can only be regarded as undesirable.

Acknowledgements: This study was funded by the Water Authority of Western Australia; we thank P Helsby of the Albany branch for his assistance. Special thanks go to G Kendrick, J Nielson and M Platell for their assistance with species identifications. Thanks also go to the two anonymous referees who provided useful comments on the manuscript.

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Contributions of N H Speck to the biogeography of Proteaceae in Western Australia

N Gibson¹, G J Keighery¹ & B J Keighery²

¹ Science and Information Division, Department of Conservation and Land Management, PO Box 51 Wanneroo WA 6065; email neilg@calm.wa.gov.au and gregk@calm.wa.gov.au

² Department of Environmental Protection, PO Box K822, Perth WA 6842; email bronwen_keighery@environ.wa.gov.au

Received January 1997; accepted May 1997

Abstract

When considering the study of the biogeography of the Western Australian flora, botanists such as Diels, Gardner and Beard spring to mind, but what has not been generally recognised outside of Western Australia was the substantial contribution of Dr Nathaniel Speck. Speck was the first to quantify patterns of species richness for the Proteaceae in south-western Australia. In addition he provided detailed community mapping of the Swan Coastal Plain in particular, and of the south west in general. Speck was also the first to propose that the Mt Lesueur region (one of the two major centres of biodiversity in Western Australia) should be recognised as a separate botanical district.

The biogeographic patterns of the Proteaceae reported by Speck are compared here to a recent synthesis based on over 21000 collections held in the Western Australian Herbarium. The current analysis was largely consistent with the Speck's 1958 work, except that the gradients in species richness away from the two major centres of species richness are less steep than previously described. This strong correlation between the two studies is despite a taxonomy that recognises more than twice the number of taxa that he dealt with and availability of many more collections across the south west.

A brief outline of Speck's botanical and ecological work and a bibliography of his published and unpublished work are included.

Introduction

The diversity and richness of the Western Australian flora have long been recognised (Diels 1906; Gardner 1944; Hopper 1979), as has the biogeographical patterning of the flora (Diels 1906; Speck 1958; Beard 1980, 1990). While the names of Diels, Gardner and Beard are readily recognised, the contribution of Nathaniel Henry Speck has often been overlooked outside of Western Australia. Speck mapped the vegetation pattern on the Swan Coastal Plain in the early 1950s and he later extended this across the whole of the southwest (Speck 1958). Based on this work he proposed that the Lesueur region should be recognised as a separate botanical district. Beard's (1980, 1990) phytogeographic mapping did not accept this division, but recent work on the biogeography of the genus *Banksia* has strongly argued for the resurrection of this district (Lamont & Connell 1996).

The detailed biogeographic patterning of many of the major genera and families is now well documented across the south-west of Western Australia (Speck 1958; Hopper & Maslin 1978; Hopper 1979; Taylor & Hopper 1988; George 1991; Keighery 1996; Lamont & Connell 1996). Speck's (1958) analysis of the biogeography of the Proteaceae was the first study to quantify these patterns. It is now almost 40 years since this ground-breaking work was published, and here we compare the results of his 1958 study with our present understanding of bio-

geography of the Proteaceae based on collections held in Western Australian Herbarium.

Methods

Speck (1958) mapped 426 taxa of the Proteaceae across the southwest on a 50000 yard (28 mile) grid, and distribution patterns were analysed on both a genus and family basis. A comparable recent analysis was compiled from distribution data for 882 taxa (in 17 genera and 779 species) based on collections held in the Western Australian Herbarium. Over 24000 collections of Proteaceae are held in the herbarium and in excess of 21000 have geographic coordinates that could be used in this analysis. Distribution patterns were determined on a one degree latitude and longitude grid basis across the State. This grid was both larger and more extensive than that used by Speck (1958). Analyses were undertaken for all taxa and for *Grevillea*, *Lambertia* and *Adenanthos*. These were compared with Speck's (1958) earlier analysis.

Results and Discussion

Comparison of biogeographic patterns

Speck's (1958) analysis of the 426 taxa of Proteaceae showed two centres of species richness, one on the northern sandplain centred on the Mt Lesueur area and a second on the south coast stretching from the Stirling Range to the Fitzgerald River area (Fig 1).

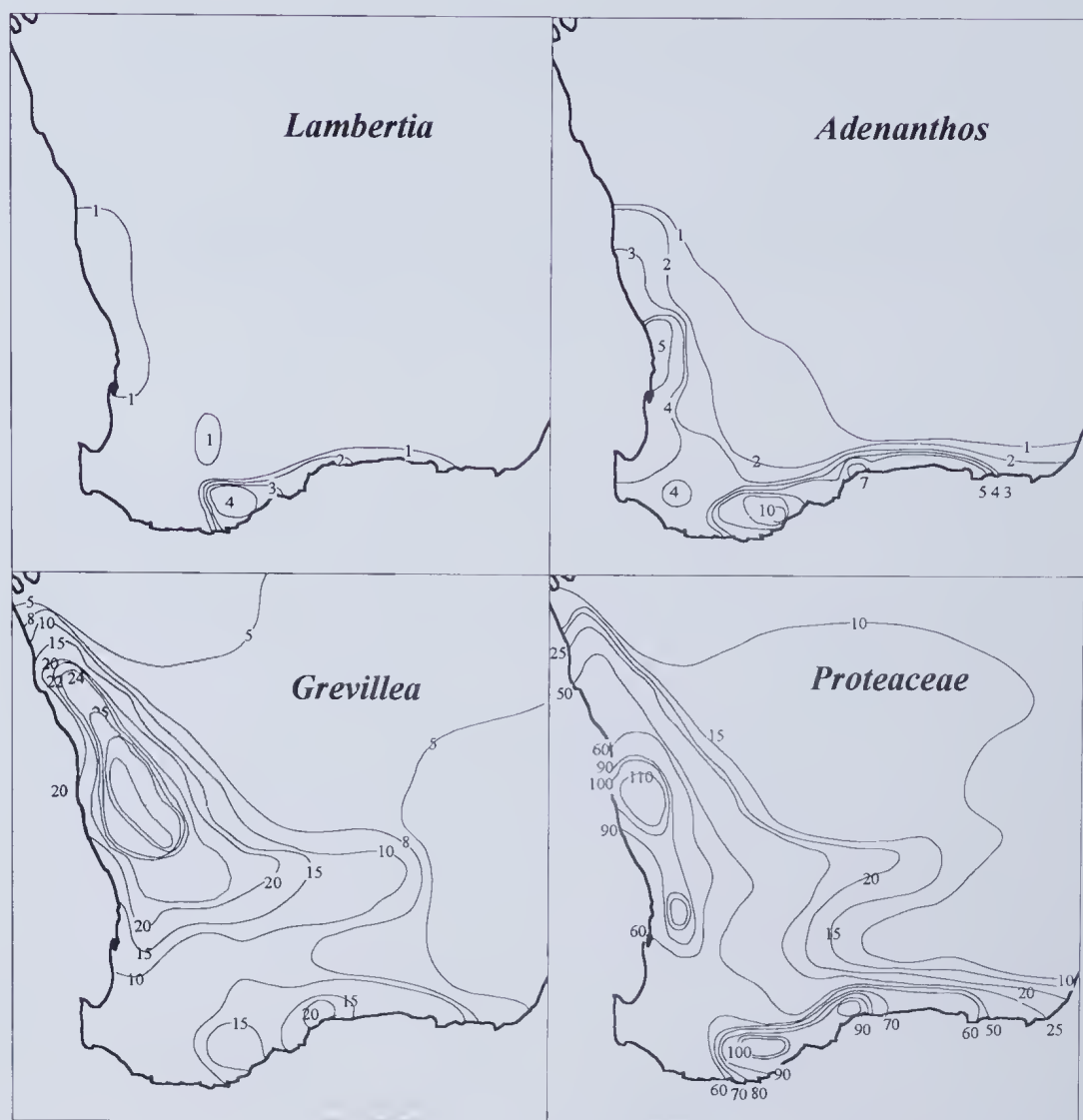


Figure 1. Isoflor maps from Speck (1958) based on a 50000 yard grid; A) *Lambertia*, B) *Adenanthos*, C) *Grevillea* and D) *Proteaceae*.

Some of the small genera such as *Adenanthos* and *Lambertia* exhibited only one main centre of species richness on the south coast while the larger genera such as *Grevillea* exhibited a bimodal pattern of species richness, as did the family as a whole (Fig 1). At both the genus and family level, a feature of the pattern that Speck (1958) showed was the very steep nature of the isoflor gradients away from the centres of species richness.

The more recent analysis of 21000 records held in the Western Australian Herbarium (Fig 2) confirms the general pattern described by Speck (1958). The main difference between the two analyses is the estimate of number of taxa at the centres of species richness (180-194 taxa per grid cell in the current analysis compared with 110-132 taxa per grid cell in Speck's analysis) and the more gradual nature of the species richness gradients now seen. These differences are accounted for by a taxonomy that now recognises more than twice the number of entities recognised in 1958, and the huge increase in collections and access across the south-west that have become available over the last 40 years. The state-wide analysis also

shows a small but significant concentration in the Kimberley region, an area not covered by Speck's earlier analysis (Fig 2).

Both analyses show evidence of sample bias. In Speck's (1958) analysis there is a large bulge along Great Eastern Highway that runs from Perth to Kalgoorlie, indicating the poor access north and south off this transport corridor in 1958. The bias in the recent analysis is more subtle, but the small peaks in the arid zone reflect either range systems or major conservation reserves. As a result, it is not possible to unequivocally attribute these small peaks to particular landforms.

Speck (1958) concluded that his isoflor maps supported the theory that the two major centres of high species richness are the centres of origin of the *Proteaceae* in the southwestern flora. His prediction that the genera of the *Myrtaceae* and *Epacridaceae* would reveal essentially similar patterns have been borne out (George 1991; Keighery 1996). Speck (1958) further argued that the high degree of endemism and species richness indicate that these centres of origin were of greater age than if they

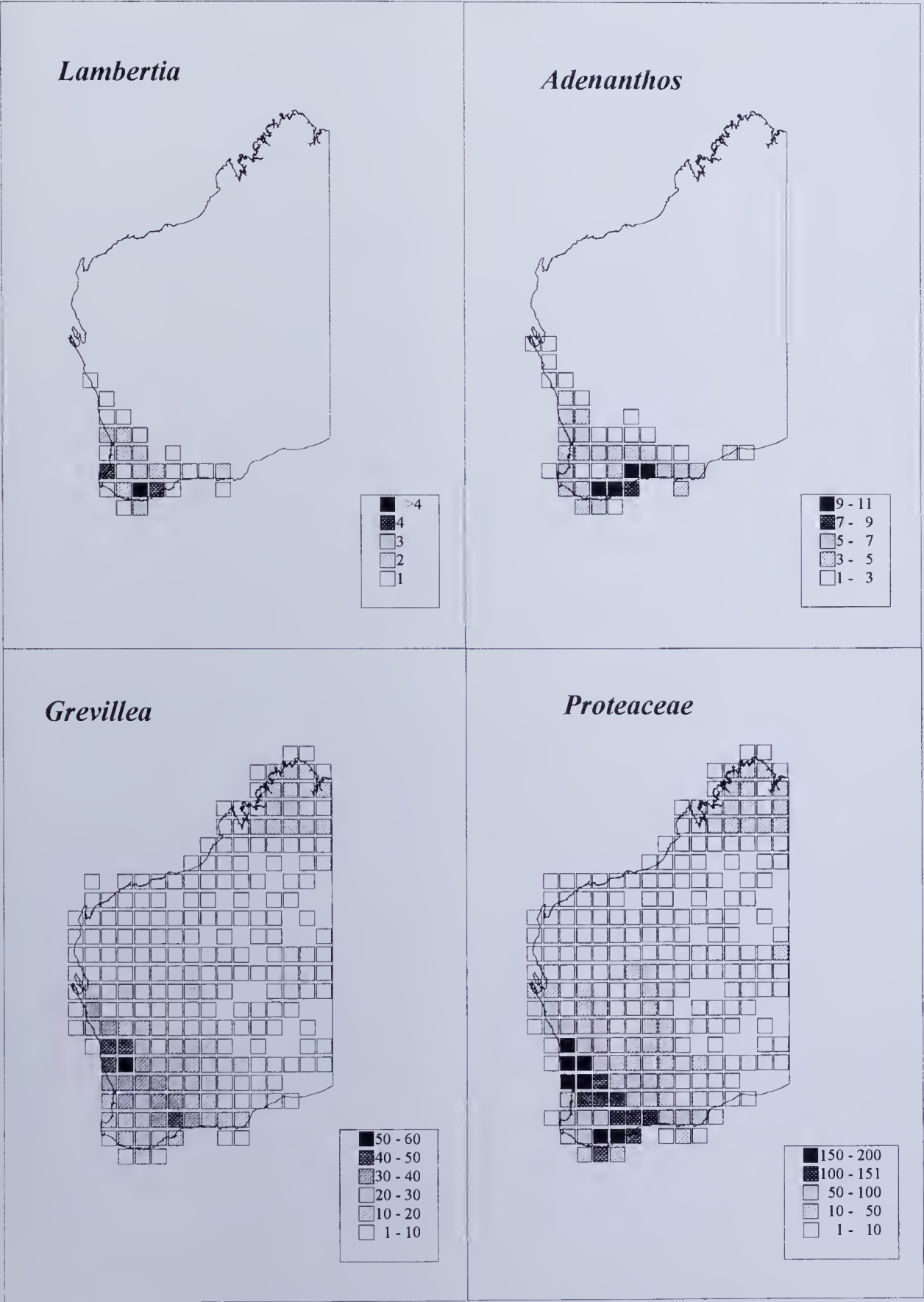


Figure 2. Isoflor maps from a recent analysis of 21000 collections held in the Western Australian Herbarium using one degree grid; A) *Lambertia*, B) *Adenanthos*, C) *Grevillea* and D) *Proteaceae*.

were only refugia and centres of redistribution following an ameliorating climate from the Last Glacial. Hopper's (1979) review of species richness across the southwest suggested that the transitional rainfall zone (in which the two centres of species richness are found) have had an extremely long history of changing climate and the species diversity of this region is a function of the both the stability of the landscape and the repeated pattern of sweeping climatic change, echoing Speck's conclusions of some 20 years previously.

In addition to his analysis of distribution patterns in the Proteaceae, Speck also undertook structural mapping of the vegetation communities across the southwest. He recognised 62 community types in 26 vegetation systems. Using these 26 vegetation systems he proposed modifications to the phytogeographic districts of Diels (1906). These modifications included the eastward movement of the Coolgardie and Austin boundary and the inclusion of a separate Lesueur district. Speck split his southern node of species richness between the Stirling district (which includes the Stirling Range) and the Eyre district (which includes the Fitzgerald River area). Beard's (1980, 1990) later mapping did not recognise the Lesueur district and incorporated all of the southern node of species richness (stretching from the Stirling Range to Fitzgerald River) into his Eyre district.

In a recent analysis of the pattern of biogeography of the genus *Banksia*, Lamont & Connell (1996) argue for the recognition of the Lesueur district, a south Stirling district and a west Eyre district corresponding to centres of *Banksia* species richness and similarity. Our current analysis was undertaken at a coarser scale than that of Lamont & Connell (1996), and only considered species richness; nevertheless, the northern node of species richness seen in our data (Fig 2) is centred on their Lesueur node (Fig 6b in Lamont & Connell 1996). At the one degree grid scale used in our analysis, no subdivision of the southern node of species richness is evident (Fig 2). While phytogeographic boundaries are not based on species richness criteria our data lends some support to a reappraisal of the status of the Lesueur phytogeographic district.

A synopsis of Nathaniel Speck's botanical career

Nathaniel Henry Speck was born in South Australia on 6 December 1906 and died in Canberra in 1970. Speck was one of those rare people who built two successful careers during his life time. The first as a science teacher then secondly as a botanist and ecologist. He began his second career with a BA degree majoring in botany which he started in 1942 at the age of 35. He graduated from the University of Western Australia in 1948. Between 1949 and 1952 he worked on his masters dissertation in which he described and mapped the major plant communities of the Swan Coastal Plain around Perth. At this time he was also responsible for the establishment of the Herbarium at the Botany Department of the University of Western Australia, which played a major role in the development of the illustrated key to the Western Australian flora produced by Blackall and Grieve (Grieve 1953). Speck was awarded his MSc in 1952. He immediately enrolled as a PhD candidate and in 1953 was

awarded a Senior Research Fellowship. His PhD topic was very ambitious; he attempted to describe and map the vegetation communities of south-western Australia from Shark Bay to Esperance, and as an aside he undertook a biogeographical analysis of the family Proteaceae across this region.

During this time he continued to assist Professor Grieve with preparation of the illustrated key to Western Australian flora, in redrawing and redrafting some of Blackall's earlier illustrations, and by taking many colour photographs for illustration of those volumes (Grieve 1953).

In July 1953, Speck applied for a position as a Technical Officer with CSIRO's Land Research and Regional Survey Section. It appears that CSIRO was so impressed with his application that they readvertised the position at a Research Officer level and Speck was offered this position, which he subsequently accepted in November 1953 at the age of 47. He and his family moved to Canberra where he commenced work as a Research Officer Grade 3 - Ecologist on 5 April 1954.

Speck immediately fitted into the survey section and undertook field work in the Gilbert-Leichardt area, around Wiluna, Western Australia and in the west Kimberley. He was made permanent in November 1954, and reclassified to Senior Research Officer in 1957. Reports of his ability and performance in CSIRO over this period are uniformly glowing.

Speck was awarded his PhD in 1959 from the University of Western Australia. His thesis was in two parts. Volume 1 described and mapped 62 plant associations in 26 vegetation systems across the southwest of Western Australia. The second volume mapped the distribution of 426 species of Proteaceae across the same area on a 50000 yard grid, and for the first time quantified the patterns of diversity of this family. It is unfortunate that Speck never formally published any of this work and this probably cost him the national and international recognition that he certainly deserved. Speck was by that time 53 years old. His work commitments in a senior position in CSIRO protracted the completion of his thesis which he initially expected to complete it in two or three years before his appointment to CSIRO. It in fact took him over six years to complete.

In the last few years of his professional life, Speck undertook consulting work as a survey ecologist for the United Nations Food and Agriculture Organisation and the UN Development Program in Argentina while on unpaid leave from CSIRO. He retired from CSIRO at the age of 60 on 2 February 1966.

In his second career Speck made a major contribution to the fields of botany, ecology and biogeography in Australia. He made over 8500 collections of which over 1800 are lodged in the Western Australian Herbarium. His published ecological work covered areas as diverse as the Swan Coastal Plain to the north Kimberley to Queensland (Appendix 1). He collected four type specimens (*Eremophila congesta* ms, *Thysanotus speckii*, *Conostylis crassinervia*, *Grevillea makinsonii*) of which the *Thysanotus* bears his name. He had a life long interest in botany and ecology, collecting and drawing plants wherever he lived. His type collection of *Grevillea makinsonii* was made

the year before he died. With his passing in 1970 at the age of 63, Australia lost one of our most significant but unrecognised field ecologists and plant biogeographers.

In his second career, Speck made a very significant contribution to the knowledge of plant biogeography in Western Australia, so much so that many of his insights are now considered common knowledge. Perhaps there is no greater accolade.

Acknowledgments: We would like to thank librarians L Wright and B Waugh for their help in locating material related to Dr Speck, Dr Speck's family for permission to access his University file and M Lyons for drafting the figures. This paper is based on a presentation prepared for the Proteaceae Conference held in Melbourne in 1996.

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Appendix 1.

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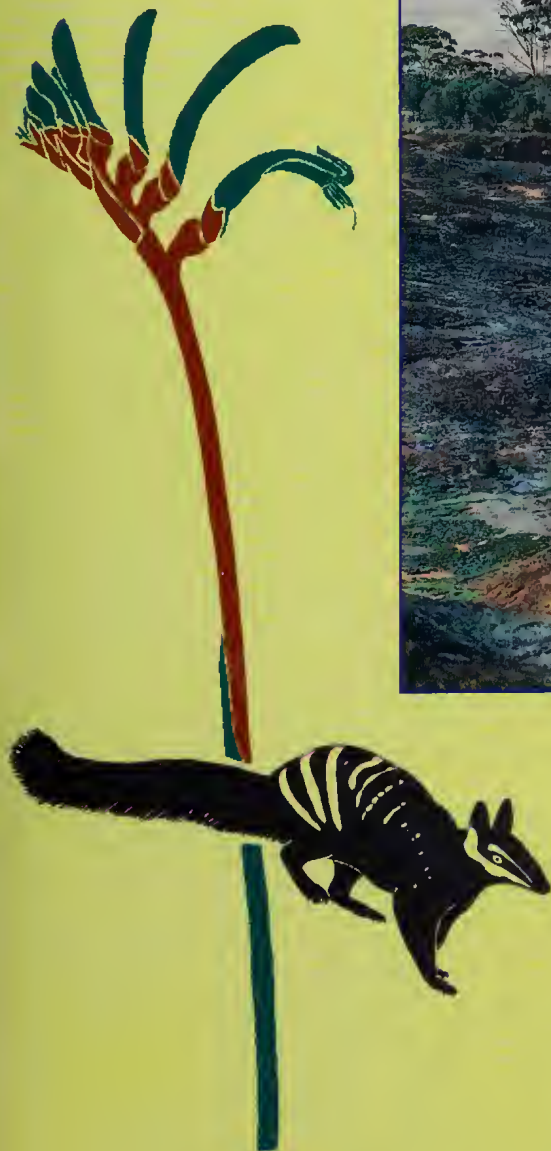
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Volume 80 Part 3
September 1997



ISSN 0035-922X

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The journal of the Royal Society of Western Australia was first published in 1915. Its circulation exceeds 600 copies. Nearly 100 of these are distributed to institutions or societies elsewhere in Australia. A further 200 copies circulate to more than 40 countries. The Society also has over 350 personal members, most of whom are scientists working in Western Australia. The Journal is indexed and abstracted internationally.

Cover design: Mangles' kangaroo paw (*Anigozanthos manglesii*) and the numbat (*Myrmecobius fasciatus*) are the floral and faunal emblems of Western Australia. Also depicted is a collection of living stromatolites which are of particular significance in Western Australian geology. The three subjects symbolize the diversity of sciences embraced by the Royal Society of Western Australia. (Artwork: Dr Jan Taylor).

Granite Outcrops Symposium

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Geology of granite

J S Myers

Geological Survey of Western Australia, 100 Plain Street, East Perth
WA 6004 email: j.myers@dme.wa.gov.au

Abstract

The genesis of granite is intimately related to the dynamic structure of the Earth. Granite is the main component of continents; it is one of the oldest known rocks; and the geological history of granite provides the main evidence about the growth and evolution of continents through time. Granite formed in a number of different situations. Some granite was generated in zones of rifted continental or oceanic crust, but most granite was generated in zones of collision between continents and oceanic crust, and where continents were amalgamated. Granite formed by two different processes: by fractional crystallization of basaltic magma; and by melting older continental crust. Between these end members, there is a spectrum of hybrid processes, including mixing of basaltic and granitic magmas, and contamination of basaltic magma by partial melts of different kinds of continental crust. Although superficially simple and similar, most granites reflect a complicated history of multistage, hybrid processes. This complexity has led to a diversity of interpretations, and the origin of granite has been one of the most hotly debated topics in geology.

The following review outlines the nature and diversity of granite; where, how, and when granite was generated; how it was intruded through the crust; the structures that it formed; and the history of debates over its origin.

What is Granite?

Granite is one of the most abundant, and most widely known, rocks on Earth. The continents are dominated by granite; it forms the most ancient cores of long eroded continents, as well as lofty peaks of the youngest mountain ranges.

Granite is an igneous rock comprising crystals of quartz, feldspar, mica and/or hornblende or pyroxene. The crystals are generally large (a few mm); they can be seen directly on outcrops, and give granite its rough texture on weathered surfaces. If most crystals are of similar size, a granite is described as even grained. If a granite contains very large crystals of feldspar (0.5 – 3.0 cm long), set in an even grained matrix, it is described as **porphyritic**, and the very large crystals are called **phenocrysts** (Fig 1). The crystals in granite are large because granite crystallized slowly from molten rock (**magma**), over 2 km below the Earth's surface. Where the same magma escaped upwards, and was erupted through fissures or volcanoes, it crystallized rapidly, forming small crystals or glass, and produced volcanic rocks.

The colour of most granites ranges from pink to cream, white and grey, and generally reflects the colour of the dominant feldspars. Many granites contain straight, parallel-sided, cream or pink veins of **pegmatite** (Fig 1). This is generally a very coarse grained variety of granite that crystallized from residual granitic magma in cracks that formed during, or soon after, the solidification of the host granite.

Quartz and feldspar are the dominant minerals in granite, and together make up 90% of the rock. Quartz

itself generally ranges from 20-45% and feldspar up to 60% of the granite. The proportions of these minerals, and the kinds of feldspars, are used to divide granites into a number of types. Feldspars are aluminosilicates



Figure 1. Typical outcrop of (porphyritic) granite in Western Australia. The rock comprises large, short tabular (white) feldspar crystals (phenocrysts) in an even grained matrix of smaller crystals of biotite (black), quartz (white), and feldspar (white). The granite is crossed by a number of white pegmatite veins, comprising quartz and feldspar crystals that grew in fissures as the fissures opened. The granite is about 2700 million years old, and is located about 120 km northwest of Meekatharra.

that contain a range of calcium, potassium and sodium. They are divided into two groups on the basis of these three elements: potassium or alkali feldspar, and plagioclase that itself ranges from calcium-rich to sodium-rich end members.

Granite *sensu stricto* is rich in potassium feldspar (up to 65% of feldspars) relative to plagioclase, and has a high content of quartz (20-60%). With increasing plagioclase/potassium feldspar ratio, and increasing calcium/sodium ratio in plagioclase, granite grades into rocks called granodiorite (plagioclase 65-90% of feldspars) and tonalite (plagioclase 90-100% of feldspars). With decreasing quartz content (quartz less than 20%), granite grades into (potassium feldspar - rich) syenite, monzonite, and (plagioclase-rich) quartz monzonite. For simplicity in this review, all these rocks of the granite family are referred to broadly as granite. They are all generally massive, coarse grained rocks, and form similar kinds of outcrops.

Granite Generation in a Dynamic Earth

The crust of the Earth is divided into two types, continental and oceanic. The continents are generally 30-40 km thick and mainly consist of granite, whereas the crust beneath the oceans is generally 5-10 km thick, and mainly consists of basalt. Granite largely consists of silica (65-75%) and has a lower density (average 2.7) than more iron- and magnesium-rich basalt (average

density 3.0) with only 50% silica. Therefore the continents are more bouyant, more elevated, and thicker than oceanic crust.

The main structure of the Earth is shown in Figure 2. Both the oceanic and continental crusts of the Earth are relatively thin, and their thickness is exaggerated in this illustration. They float on a region of ductile, semi-molten rock called the **Mantle**, and below that lies a ductile Outer Core and a more rigid Inner Core of iron and nickel. Heat generated by radioactive decay leads to **convection** within the Mantle.

Rift zones

Where convection currents rise and move apart, the thin crust is split, and basaltic magma is erupted through the resulting fissures. Where this occurs beneath the oceans along mid-ocean ridges, more oceanic crust is generated. Most of this remains submerged, except locally where the submarine mountain chains rise above sea level, or where the oceanic crust is abnormally thick, such as in Iceland (Fig 3).

In some cases, the magma collects in pools deep in the crust and starts to crystallize. The first crystals to form, dense iron and magnesium - rich minerals (olivine, pyroxene, and spinel), may sink in the magma and accumulate at the bottom of these magma chambers. Thus the composition of the residual magma gradually becomes relatively richer in silica and alumina. This process is called **fractional crystallization** and leads to the generation of a variety of igneous rocks.

Only a small amount of granite is generated in this situation where oceanic crust is pulled apart, but where continents are pulled apart some of the older continental crust may be partly melted and rise as granitic magma. A good example of this can be seen on the east coast of Greenland which was rifted from northwest Europe about 53 million years ago as the Atlantic Ocean started to form. Basaltic magma was erupted through steep fissures called **dykes** in the splitting continental crust (Fig 4). The magma was erupted as lava flows over the subsiding edges of the rifting continent and formed extensive piles of basalt several kilometres thick. These basalt flows are well preserved in East Greenland and in northwest Britain, including the famous localities of the Giant's Causeway in Ireland, and Fingal's Cave on Staffa in Scotland.

Some basaltic magma that remained in pools within the crust crystallized slowly as gabbro (Fig 6), the coarse grained equivalent of basalt. Many of these gabbros are compositionally layered and show fractional crystallization. In some places fractional crystallization of basaltic magma, and partial melting of the continental crust, generated granitic magma (Fig 5).

Collision zones

Most granite was not formed in rift situations, but where Mantle convection currents converged. There the crust was pushed together and thickened, and the deeper parts melted. The two main situations are shown on Figure 2;

1. continent/oceanic crust collision in which granite was generated in a number of stages, and intruded passively into extending crust, and

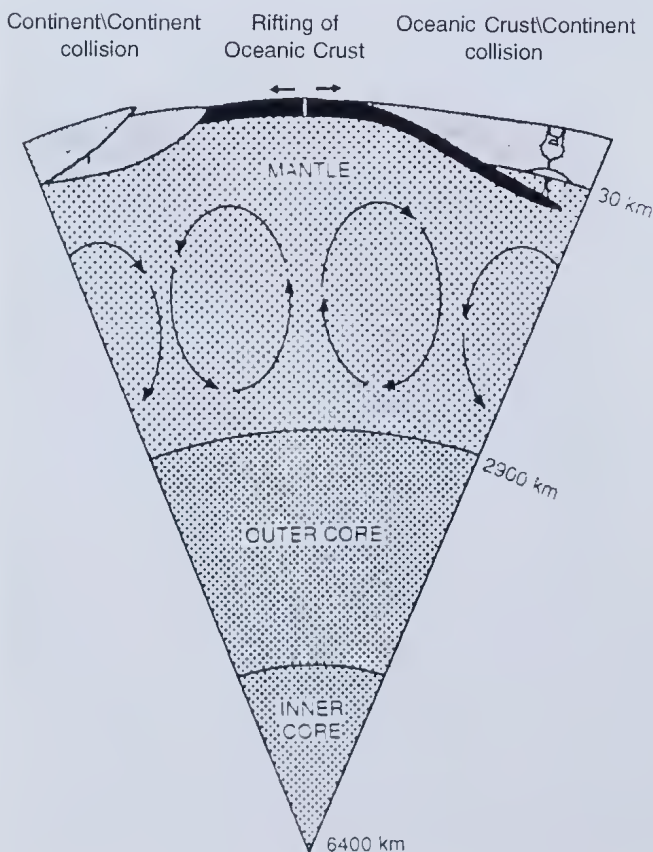


Figure 2. Section showing the main structure of the Earth.



Figure 3. Basalt lava (grey) forming extensive flows and small volcanic cones that were erupted between 1725 and 1729 AD at Krafla in northeastern Iceland. Iceland is located on the mid-Atlantic ridge that marks rifting between North America and Europe. The small valley extending between the volcanic cone in the left foreground and the cone on the far right, lies along the axis of the main rift, and formed during an episode of rifting at about 1725 AD. The darker, new lava, in the vicinity of the fumaroles in the centre and left centre of the photograph, was erupted in December 1975 at the start of a new phase of rifting and volcanic activity that continues to the present. View to the north in July 1977.



Figure 4. Black dykes of basalt intruded into fissures in much older (*ca* 2800 Ma) granitic gneiss, during initial rifting between North America and Europe. Headland between Tasilaq and Østre Tasissaq, west of Kap Gustav Holm, East Greenland. The mountain is 1000 m high.



Figure 5. Granite generated during continental rifting between North America and Europe. The mountain exposes the upper, dome-shaped portion of a circular granite body (white), intruded into black diorite 35 million years ago. Thin sheets of granite occur in the diorite parallel to the roof of the main granite. Auluiartik island, Kialineq, East Greenland. The mountains are 500 m high.



Figure 6. Igneous layers rich in plagioclase feldspar (pale) or pyroxene (dark) in uniform gabbro, formed during the crystallization of basaltic magma. The magma was intruded into an opening cavity at the base of a thick pile of basalt lava flows (forming the upper parts of the mountains), during initial rifting between North America and Europe about 53 million years ago. Skaergaard Intrusion, East Greenland.

2. continent/continent collision in which granite was generated directly by melting of continental crust, and was intruded as sheets that were deformed during and after crystallization.

Continent/Oceanic Crust Collision

The main features of continent/oceanic crust collision are shown in Figure 7. Oceanic crust is pushed down into the Mantle below the continental crust, forming a structure called a **subduction zone**. At depth, within this zone, the oceanic crust melts, and also introduces saline fluids which induce melting in the overlying Mantle. The melts are basaltic in composition. They collect, rise, and spread out in the lower crust where they may crystallize as gabbro, or form granitic magma by fractional crystallization and contamination with

melting continental crust. The granitic magmas collect and rise to form large bodies that may fractionate further, forming a whole spectrum of different granitic magmas that, with increasing contents of silica and alkalis, may crystallize as tonalite, granodiorite and granite.

Granite intrusion processes

In the lower, ductile, part of the continental crust, granitic magma may rise as diapirs that push aside the adjacent rocks (Fig 8). In higher, semi-ductile, parts of the crust, where the magma can no longer rise diapirically, it may spread out to form bodies with flat floors and dome-shaped roofs called **laccoliths** (Fig 8). In the upper, brittle, part of the crust, granitic magma is intruded along fractures (Figs 8 and 9). In some cases the fracturing leads to the collapse of large blocks of crust, with dimensions of several kilometres, that founder into underlying pools of magma. The magma rises up the vertical fractures and fills the space being created by the sinking block. This is the main process by which large volumes of granitic magma are intruded to high levels in the crust, and is called **cauldron subsidence** (Figs 8

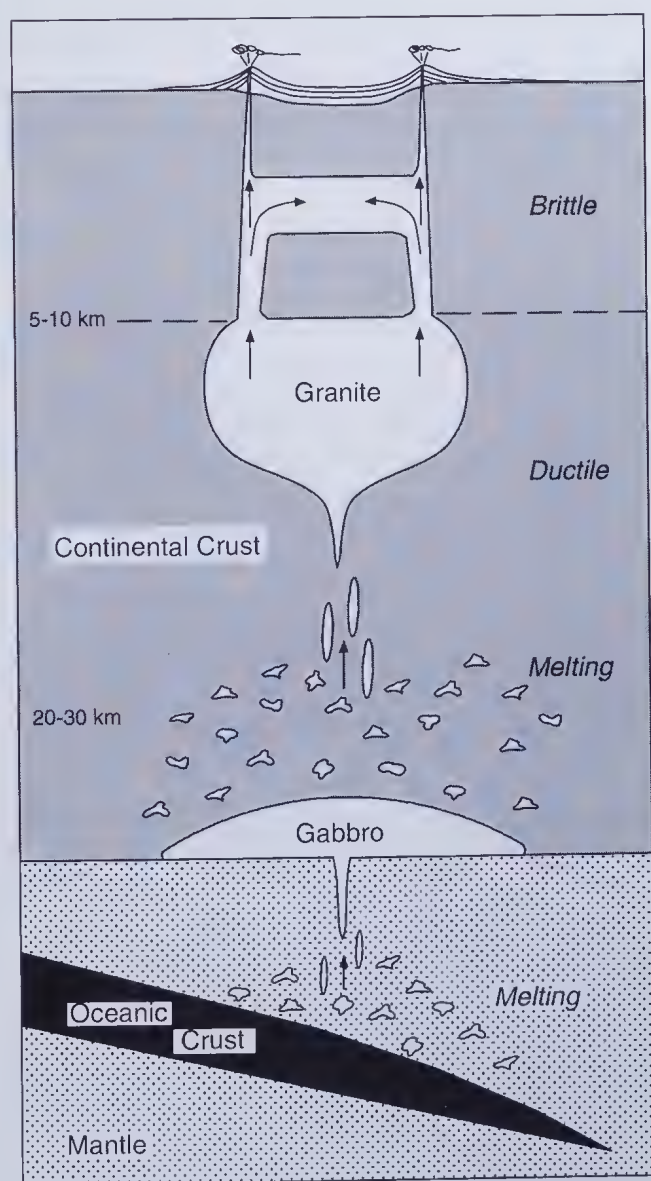


Figure 7. Schematic crustal section showing the generation and intrusion of magmas above a slab of oceanic crust subducted below a continental margin.

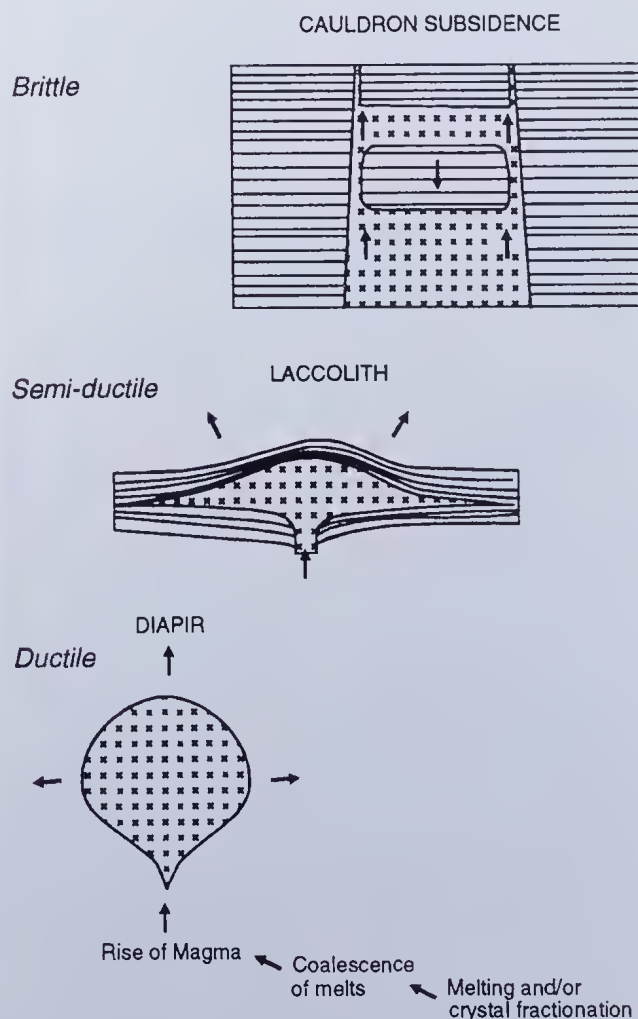


Figure 8. Schematic sections showing modes of granite intrusion at different crustal levels.

and 9). The process of fracturing of the older rocks around granite intrusions is called **stopping**, and leads to the incorporation of angular fragments of wall and roof rocks into granitic magma chambers (Fig 10). These rock fragments are trapped in the granite as it solidified and are known as **xenoliths** or inclusions.

Inclusions can also arise by a completely different process. In many instances, dykes of basaltic magma were intruded from deeper magma chambers up through and into granite plutons and crystallizing bodies of granitic magma. Where the granite was already solidified, the basaltic dykes crystallized in the straight fractures into which they were intruded. But where the granite was still a mixture of liquid and crystals, the dykes, after intrusion as linear bodies along shock induced fractures, broke up into linear trains of globular fragments called **pillows** within the still unconsolidated granite (Fig 11).

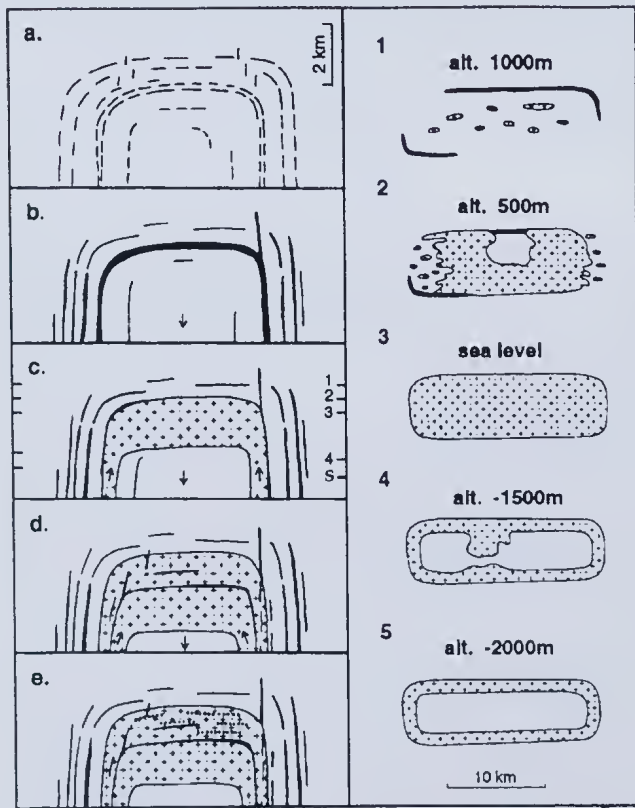


Figure 9. Left: Vertical sections showing progressive stages a - e in the intrusion of granite by cauldron subsidence in the Coastal Batholith of Peru. a: fractures define the framework of cauldron subsidence; b: turbulent mixtures of gas and magma (black) move up the fractures; c: the central block of older rocks (white) subsides and granitic magma (crosses) is intruded into the opening space; d: the granite body is displaced downwards by a second episode of cauldron subsidence; e: flat-lying sheets of pegmatite (dots) are intruded into the roof region of the second granite body during further slight subsidence. Right: Horizontal sections of the granite plutons at the five levels marked on section c.



Figure 10. Angular fragments of older rocks (stippled) incorporated by stopping into granite (white) 66 million years ago. Puscao granite, Coastal Batholith of Peru, 25 km ESE of Huarney.

Granite structures and cordilleran batholiths

Magma generated along subduction zones rise to form narrow, linear belts, generally 50 - 100 km wide and thousands of kilometres long. These belts occur within, and parallel to, the margins of continents. The Andes (Fig 12) provides one of the simplest examples. Here, in a head-on collision, the South American continent is being pushed over Pacific oceanic crust. This situation has existed for over 100 million years, and Figure 12 shows the extent of granite and associated volcanic rocks generated during this time by the processes shown on Figure 7.

The granites and volcanic rocks form a major part of the Andes, and in Peru their structure can be clearly seen in mountainous desert with steep relief of 5 km (Fig 13). The granite bodies have steep walls and flat roofs. The cross section, Figure 14, shows some of the complexity of repeated granite intrusion by cauldron subsidence into the same 50 km wide belt, over a period of 35 million years, between 100 and 65 million years ago. A complex of related granite bodies such as this is called a **batholith**, and batholiths that formed above subduction zones are known as **cordilleran batholiths**.

Associated volcanic debris

Here in the Andes, the granites rose into volcanic rocks derived from the same magmas. In some places they are associated with calderas, large circular depressions, up to 25 km in diameter, in which the older volcanic rocks sank into underlying bodies of magma. At the same time, large volumes of volcanic rocks were explosively erupted from circular fissures around the caldera rims. High clouds of ash, steam and gas, dropped rock and crystal fragments over vast areas, forming deposits that later solidified to form a volcanic rock called tuff. In some cases the ash columns collapsed, or the eruptions did not become airborne, and the erupted mixtures of hot gas, magma, crystals and rock fragments travelled as turbulent flows for huge distances (often over 50 km), very fast on thin cushions of gas, and left deposits of fused fragmentary volcanic rocks called ignimbrite. These deposits are widely preserved in southern Peru and northern Chile (Fig 15) where, because of extreme aridity, there has been less incision by erosion than in central and northern Peru, and southern Chile.

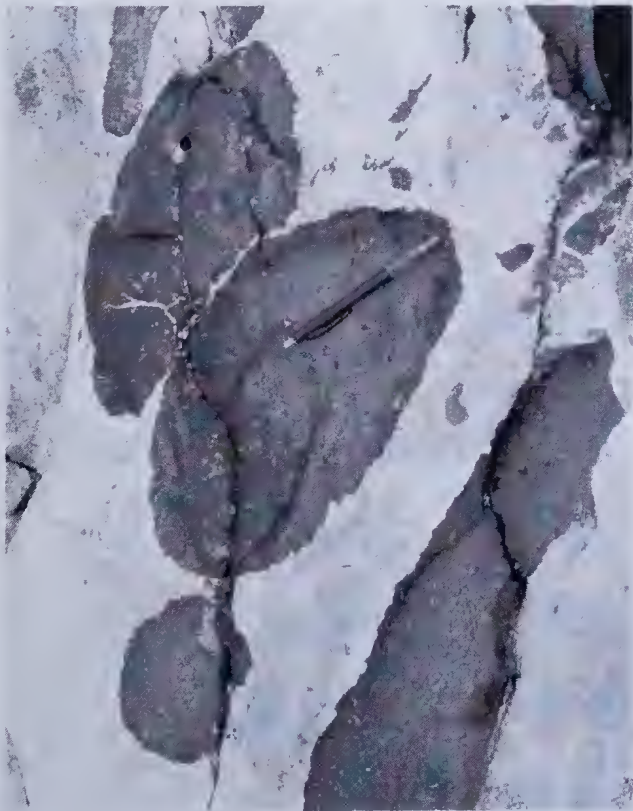


Figure 11. Black pillow fragments of a basalt dyke intruded into a granite before the granite had solidified. Note the cauliform margins of the pillows indicating that both basalt and granite were ductile when the basalt dyke was fragmented. Lilleø, Kialineq, East Greenland.

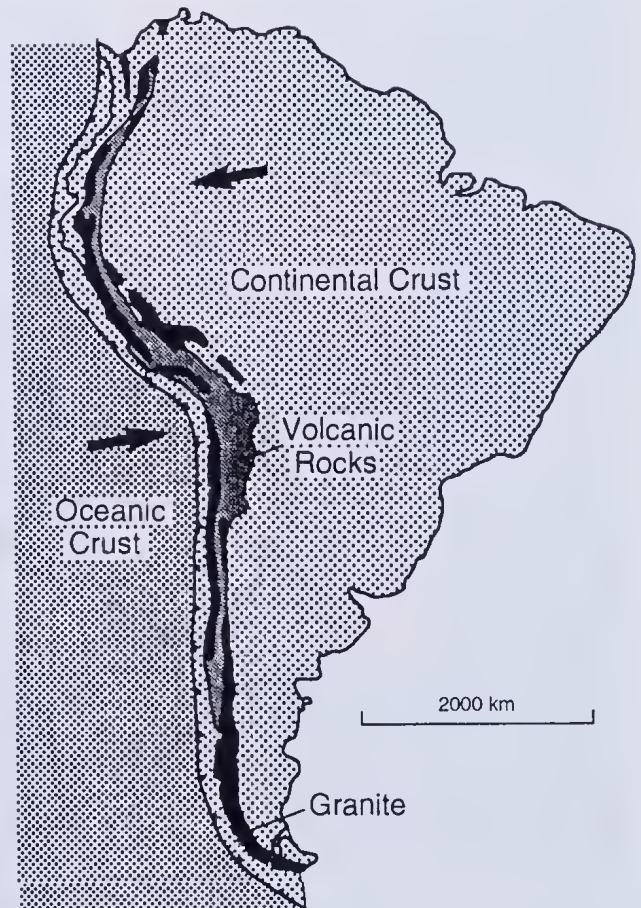


Figure 12. Map showing major outcrops of granite and volcanic rocks of the Andes, formed along the continental margin of South America where Pacific oceanic crust is subducted below continental crust. Arrows indicate the main direction of movement of the two slabs of crust.

Continent/Continent Collision

Granite was also generated from melting of continental crust where continents collided and thickened as one was pushed over the other (Fig 2). This situation is still active in the Himalayas and beneath the Tibetan Plateau where the Indian continent has already been pushed for 2000 km under the edge of the Eurasian continent during the past 50 million years.

Many continental margins involved in continent/continent collisions were preceded by episodes of continent/ocean collision in which granite was generated above subduction zones, as in the Andes. In the Himalayas, the 2500 km long Transhimalayan Batholith and part of the Karakoram Batholith (Fig 16) formed as Andean-type cordilleran batholiths above subduction zones, before the collision of India and Eurasia. In many cases, thin strips of older continental crust, ocean ridges, oceanic plateau, and basaltic island arcs such as those now forming in Java and Japan where oceanic crust is subducted below another slab of oceanic crust, were swept against a continental margin and trapped and deformed during later continent/continent collision. Therefore the structure and geological history of most continent/continent collision zones is much more complicated than those of continent/ocean collision.



Figure 13. Extensive granite outcrops forming a belt 50 km wide and 2000 km long in the Andes in Peru. View southeast along the Coastal Batholith from an altitude of *ca* 2100 m, west of Chasquitambo. The batholith was mainly intruded between 100 and 65 million years ago into coeval volcanic rocks. The volcanic rocks (black), forming the flat roof of the batholith, can be seen in the distant (left) mountain peaks, and on a chain of peaks in the distant centre within a ring dyke of granite, 1 km thick and 25 km in diameter, emplaced by cauldron subsidence. Similar volcanic rocks occur beneath the fog (distant right), where they form the western vertical margin of the batholith adjacent to the Pacific Ocean. The black rocks in the middle foreground are large fragments of gabbro that crystallized from basaltic magma before the intrusion of the granite.

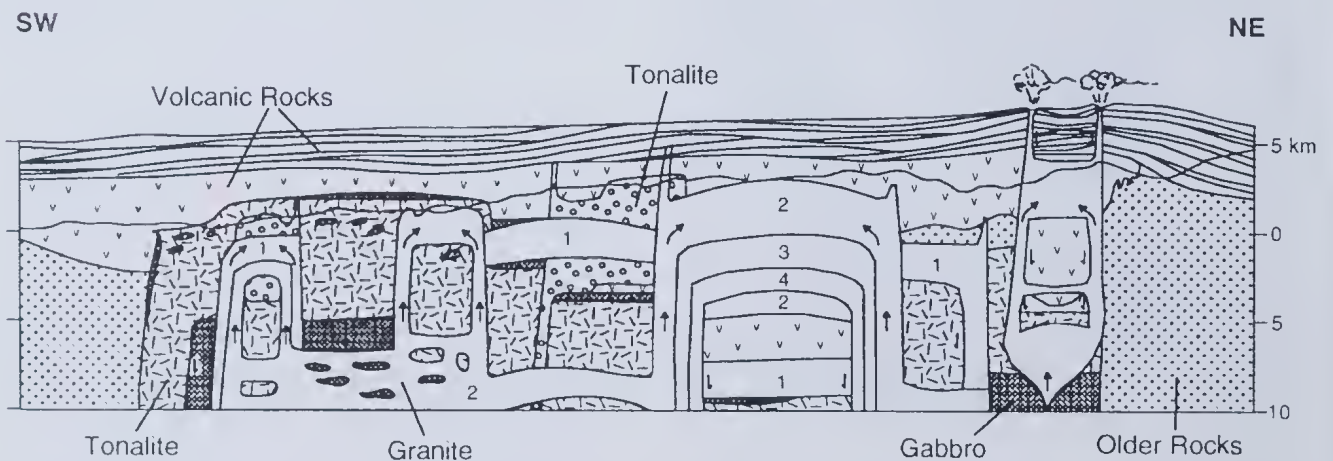


Figure 14. Vertical section across a typical cordilleran batholith showing the structure formed by repeated episodes of igneous intrusion of gabbro, tonalite and granite by cauldron subsidence into related volcanic rocks. Section across the Coastal Batholith of Peru, located due west of the word continental crust on Figure 12. Note that horizontal and vertical scales are equal.



Figure 15. Valley (foreground) incised into extensive sheets of ignimbrite, erupted from granitic magma in northern Chile. The ignimbrites were erupted from fissures parallel to the western summits of the Andes (left) and flowed down towards the Pacific Ocean (off to the right), between 10 and 5 million years ago. Volcanic cones (distant left) formed from eruptions of basalt and andesite during the past 1 million years. View south from an altitude of 4300 m between Tatío and Lasana.



Figure 16. Granite (distant snow-covered 7000 - 8000 m peaks) of the Karakorum Batholith that initially formed at c. 90 Ma during subduction of oceanic crust beneath the margin of Asia before the collision with India about 50 million years ago. View to the north from an altitude of ca 2500 m, east of Hunza, Pakistan. The Hunza valley (foreground) was incised during recent, ongoing uplift of the Himalayan range.

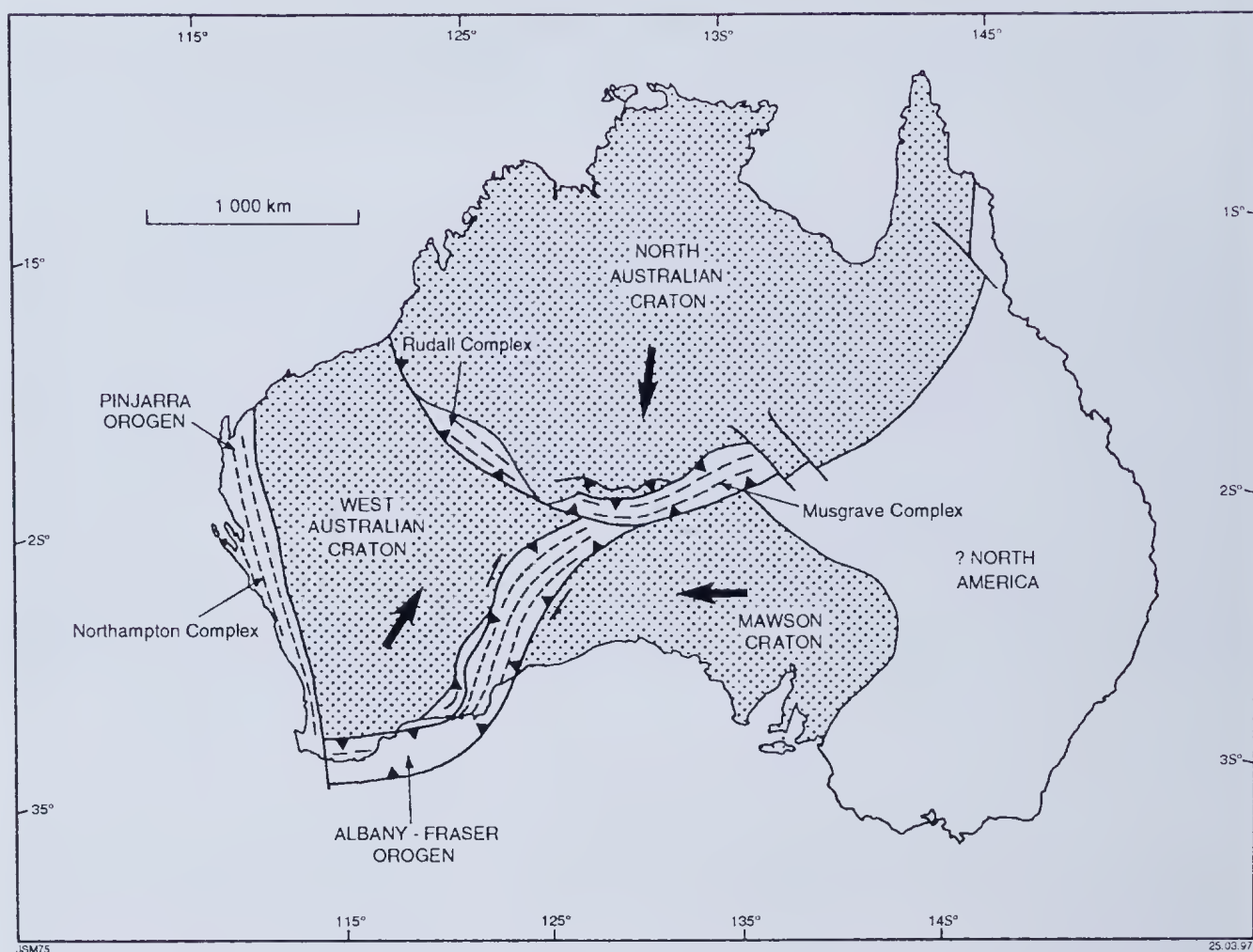


Figure 17. Map showing the assembly of three independent rafts of continental crust (cratons) 1300 million years ago, and the location of the Albany-Fraser Orogen. Arrows indicate the main directions of movement of the three continental rafts.

Albany-Fraser Orogen

Some of the products of continent/continent collision can be seen in the old, deeply eroded remnants of former mountain belts in Western Australia, such as the Albany-Fraser Orogen. About 1300 million years ago, three rafts of continental crust were joined to form a major part of what is now the Australian continent (Fig 17). The south coast of Western Australia exposes the roots of a mountain belt that formed at this time when a West Australian **craton** or continent, was joined to a combined South Australian - East Antarctic continent called the Mawson Craton. This kind of collision zone is called an **orogen**, and this particular zone is known as the Albany-Fraser Orogen.

Granite was extensively generated during two distinct episodes of this continental collision, and forms the main rock outcrops of the region. The older granite, called Recherche granite, was intruded intermittently during the collision 1300 million years ago (Fig 18). At that time the margin of the Mawson continent was being deformed and thickened as slabs of continental crust

were stacked over each other. Some of the granite was intensely deformed and recrystallized, deep in the crust. Pegmatite veins and inclusions were all streaked out into parallel layers and the granite was converted into a metamorphic rock called **gneiss** (Fig 19). There is widespread evidence that a smaller amount of granite also locally formed *in situ* by melting of older (1700 - 1600 Ma) granite of the Mawson continent, immediately after the initial episode of deformation and crustal thickening at 1300 Ma (Fig 20). This kind of metamorphic rock, comprising a mixture of older rocks with younger veins of granite, and diffuse patches of melting, is known as **migmatite**.

The younger granite, intruded about 1180 million years ago, is called Esperance granite (Fig 21), and is prominent to the east and northeast of Esperance, along the south coast from William Bay through Albany to Mount Manypeaks, and forms the Porongorups. This granite, like the Recherche granite, may be largely derived by melting of older continental crust at depth, during another episode of oblique compression in which



Figure 18. 1300 Ma Recherche Granite with angular stoped and veined fragments of previously deformed, darker, 1700 - 1600 Ma granite containing remnants of basaltic dykes. Albany-Fraser Orogen: coast south of Lake Gore, west of Esperance.



Figure 19. Banded granitic gneiss formed by intense deformation of granite and pegmatite veins (Recherche Granite) 1300 million years ago in the Albany-Fraser Orogen. Butty Head, west of Esperance.

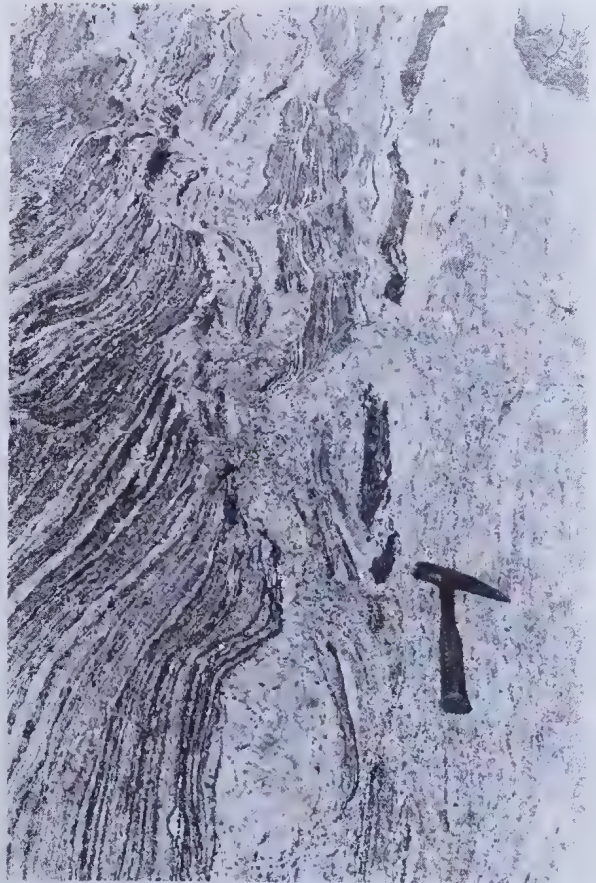


Figure 20. Irregular, diffuse veins of (pale) granite (beneath the hammer) formed 1300 million years ago by melting of older banded granitic gneiss (1650 Ma) in the Albany-Fraser Orogen. South of Lake Gidong, west of Esperance.



Figure 21. Outcrops of porphyritic Esperance granite in the Albany-Fraser Orogen, east of Esperance. This granite contains fragments of older Recherche granite, into which it was intruded 1180 million years ago. View to the southeast, at Thistle Cove, east of Cape Le Grand.



Figure 22. Map showing the main granite outcrops in Western Australia, with the ages of granites given in million years (Ma). Note that the granite in the vicinity of Cape Leeuwin is much younger than all the other granites shown.

the West Australian continent continued to slide northeastward relative to the more westerly-moving Mawson continent.

Older orogens in Western Australia

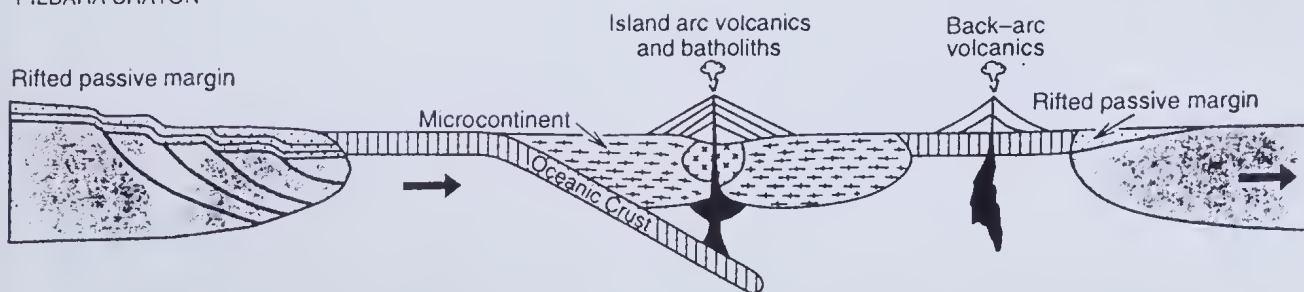
There are several remnants of even older orogens in Western Australia that mark former episodes of continental collision and granite generation. The most prominent orogens with extensive granite outcrops occur in the Kimberley region (Halls Creek and King Leopold orogens), and in the Gascoyne region (Capricorn Orogen) (Fig 22). The Capricorn Orogen marks the joining of the formerly independent Pilbara and Yilgarn continents about 2000 million years ago. Granite was generated in a cordilleran-type batholith before the collision (Fig 23), and again during and after the collision by melting of thickened continental crust.

These older Pilbara and Yilgarn continents also largely consist of granite, although in the Pilbara much of this is buried by volcanic rocks and the Hamersley banded iron formations. The most extensive granite outcrops form part of the Yilgarn Craton or continent. Most of these granites were generated by melting of older continental crust between 2700 and 2600 million years ago (Fig 1), when this continent was assembled from a number of smaller rafts of continental crust. Deformed remnants of older continental crust are exposed in the Narryer gneiss complex that forms the northwest part of the Yilgarn Craton, northwest of Meekatharra. These gneisses are largely derived from granite, including some of the oldest known rocks on Earth that formed 3600 million years ago (Fig 24).

2000 Ma

PILBARA CRATON

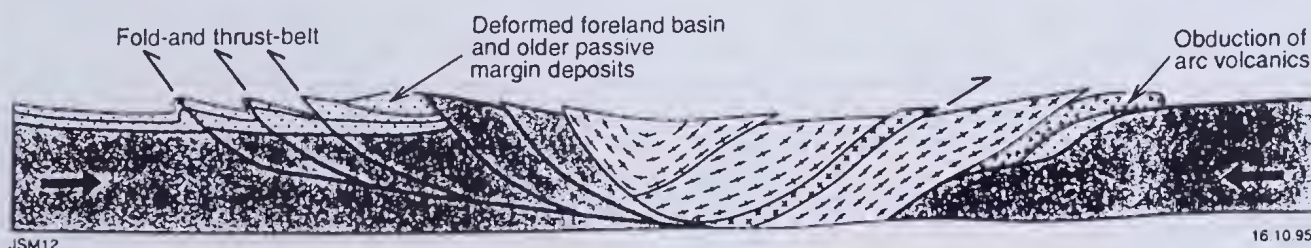
YILGARN CRATON



1850 Ma

PILBARA CRATON

YILGARN CRATON



JSM12

16 10 95

Figure 23. Schematic, vertical cross-sections showing the generation (at 2000 Ma) and deformation (at 1850 Ma) of granite (diagonal crosses) in a cordilleran batholith involved in continental collision between the Pilbara and Yilgarn cratons.

Granite in Historical Perspective

During the late 18th century, when geology was in its infancy, it was widely believed that granite was the oldest of rocks and was a precipitate from a world-wide ocean of molten rock. Supporters of this idea, advocated most strongly by Abraham Werner from the Mining Academy of Freiburg in Saxony, were known as **Neptunists**. This concept was first challenged in 1795 by James Hutton of Edinburgh who described veins of granite cutting across sedimentary rocks in Scotland, in his book "Theory of the Earth". He saw that the sedimentary rocks were baked by the granite and concluded that the granite must have been intruded as a hot liquid from subterranean regions of molten rock. His supporters were known as **Plutonists**, but were a small minority until joined by the influential Charles Lyell in the 1830s.

During the 1830s, just as Hutton's concept of the igneous origin of granite was becoming widely accepted, granite was found in many places to be closely associated with rocks that had been transformed under conditions of high temperature and pressure, deep in the Earth, into rocks that Charles Lyell called metamorphic. Various kinds of igneous and sedimentary rocks appeared to have been converted into granite by a process known as **granitisation**. This theory of granite formation became predominant during the latter part of the 19th century, and remained so until the early 1960s. Its supporters were generally known as **transformists**. This theory was widely supported in France by Michel-Levy, Lacroix, Termier and others; in Scandinavia by Keilhau and Sederholm; in Switzerland by Wegmann; and in Britain by Read. Meanwhile, during the first half of the 20th century, a minority led by the experimental and



Figure 24. Granite (below the hammer) intruded between 2700 and 2600 Ma into banded gneiss (top right), derived from much older, 3600 Ma, granite by deformation and recrystallization. Narryer gneiss complex, 170 km northwest of Meekatharra.

geochemical work of Bowen and Nockolds demonstrated the importance of fractional crystallization in producing a diversity of igneous rocks from basalt to granite.

The last 30 years has seen a general decline in the popularity of granitisation, and more popular support for an igneous origin of granite. The advent of plate tectonic theory during the late 1960s provided a framework in which a diversity of different interpretations of different kinds of granite could be reconciled.

Some granites formed by melting, or partial melting, of older heterogeneous continental crust, ranging from gabbro and granite to sedimentary rocks. Some granites formed by fractional crystallization from basaltic magmas. Many granites were derived by a combination of both processes: by fractional crystallization of basaltic magma, contaminated by heterogeneous continental crust; and by mixing of basaltic and granitic magmas.

The bulk composition and texture of many granites are superficially similar, but this often masks a complicated history of multistage, hybrid processes. Detailed geochemistry, especially of trace elements and isotopes, and detailed geochronology, especially analysis of individual zircons, are becoming increasingly important in deciphering the source rocks, the conditions of melt generation, and the evolution of granitic magmas.

Debates on the origin of granite continue. Although abundant and superficially simple, the interpretation of granite still offers exciting challenges for future generations of geologists.

References

Much of what is said here about granite can be found in current geological textbooks. In addition, a recent book by Pitcher (1993) on granite, provides a detailed account of current knowledge of granite and its historical perspective. Another overview of granite geology is given by Atherton (1993). The proceedings of a 1995 conference on granite (Brown *et al.* 1996) present a spectrum of recent work on the geology of granite. Other recent key references to Western Australian granites mentioned above are included in this selected bibliography.

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Granite landforms

E M Campbell

Department of Geology and Geophysics, University of Adelaide, North Terrace,
Adelaide SA 5005: email campbell@geology.adelaide.edu.au

Abstract

Fresh granite is low in porosity and permeability, but is highly pervious by virtue of a connected series of orthogonal and sheet fractures. Granite is susceptible to weathering by moisture, leading to the formation of a regolith. The course and rate of weathering are influenced by the structure of the rock, including fractures; mineral composition; texture, especially size of the crystals; and the physical, chemical and biotic nature of the invasive water.

Plains occupy extensive areas of granite outcrops, but positive relief forms – bornhardts, nubbins and castle koppies – have attracted most attention. Minor forms developed on granite are due primarily to weathering, *e.g.* boulders, flared slopes, rock basins, tafoni. Many of them are initiated in the subsurface. Some, like A-tents, are tectonic. Some forms are convergent as they evolve in different ways. Several are not yet satisfactorily explained.

Introduction

The aim of this review is to describe and explain the assemblage of landforms, both major and minor, characteristically developed on granite. None of these landforms is peculiar to granite: each of the forms is developed in a variety of different materials and they all have developed under a wide range of climates (Campbell & Twidale 1995a). Nevertheless, the assemblage of landforms is typical of granite, so much so that it is possible, in many circumstances, to predict from afar the nature of the underlying rock.

Weathering patterns are of primary importance in the development of many granite forms, though others are due principally to tectonic forces (see below). The interaction of granite with the atmosphere and the hydrosphere leads to weathering of the constituent minerals and the formation of a regolith. Weathering, the disintegration or alteration of rocks at and near the Earth's surface, can conveniently be divided into those processes which involve chemical reactions and the formation of new minerals (chemical weathering) and those that involve only physical breakdown of the rock (physical weathering). Most commonly, however, these several processes operate together. The type and rate of weathering of rocks depend on rock characteristics, the physical, chemical and biotic characteristics of the weathering fluids, the nature of reactions at the mineral surface and environmental factors (Colman & Dethier 1986). The base of the regolith, the contact of the regolith with the unweathered bedrock, is called the weathering front (Mabbutt 1961). The weathering front may be irregular, partly due to structural weaknesses of various types and partly as a result of the concentration of moisture.

The rock characteristics which influence the rate of weathering are fracture density, mineral composition

and texture. Being composed of interlocking crystals of quartz, feldspar and mica, fresh granite is of low porosity and permeability. Granite is pervious because water penetrates the rock along partings, especially orthogonal joints and sheet fractures. Fractures occur at all scales from microcracks within minerals to partings that can be kilometres in length. Highly fractured rocks are more susceptible to weathering than those in which the fractures are absent, widely spaced or tightly closed. In some instances, even though no fracture is discernible, the crystals may be in strain, leading to a higher susceptibility to weathering (Russell 1935).

The stability of the common silicate minerals is closely related to their order of crystallisation from a silicate melt (Goldich 1938). Minerals that crystallise at the highest temperatures, especially biotite and plagioclase feldspar, are unstable at the Earth's surface and are susceptible to alteration, and granites with a higher than average proportion of these more readily weathered minerals tend to form negative features whereas those with a greater abundance of quartz and potassium minerals, which crystallise at lower temperatures and are more stable, tend to be more resistant (*e.g.* Brook 1978). This variation in susceptibility to weathering is demonstrated at the crystal scale by the occurrence of pitted surfaces where granite is in contact with water. The biotite and plagioclase feldspars are chemically altered, leaving the quartz and potassium feldspars in relief. As the surface is rapidly reduced by flaking, such pitted surfaces are an indicator of recent exposure from beneath the regolith (Twidale & Bourne 1976a).

Variations in crystal size do not produce consistent effects (Twidale 1982). Finer-grained granites tend to be more susceptible to weathering due to the greater surface area to volume ratio of each crystal. However, coarser crystals, especially those that are in strain and hence traversed by an array of microcracks, may be more strongly weathered (Russell 1935; Pope 1995; Hill 1996).

Organisms, especially microorganisms such as bacteria, algae and lichens, significantly affect the rate of weathering of granite. Algae readily colonise rock



surfaces. Their hyphae penetrate between and within the mineral grains by a combination of physical activity and biochemical reactions (Yatsu 1988). Lichens are characteristic of granite exposures and although in humid environments they protect the surface, in arid environments they contribute to the physical and biochemical weathering of the rock (Fry 1927; Viles 1988). The retention of moisture by plants and soils, especially in fissures and basins, and the humic acids resulting from plant and animal decay also increase weathering.

The thickness of the regolith is a function of the relative rates of weathering and erosion, or the wearing away of the land surface. In most areas erosion is principally by running water. In tectonically stable regions, or those situated far from the sea, which is the ultimate base level of erosion, or those in humid tropical environments where weathering proceeds rapidly, or those in arid or semiarid environments where erosion of the regolith may be restricted, great thicknesses of regolith (100 m or more) may develop.

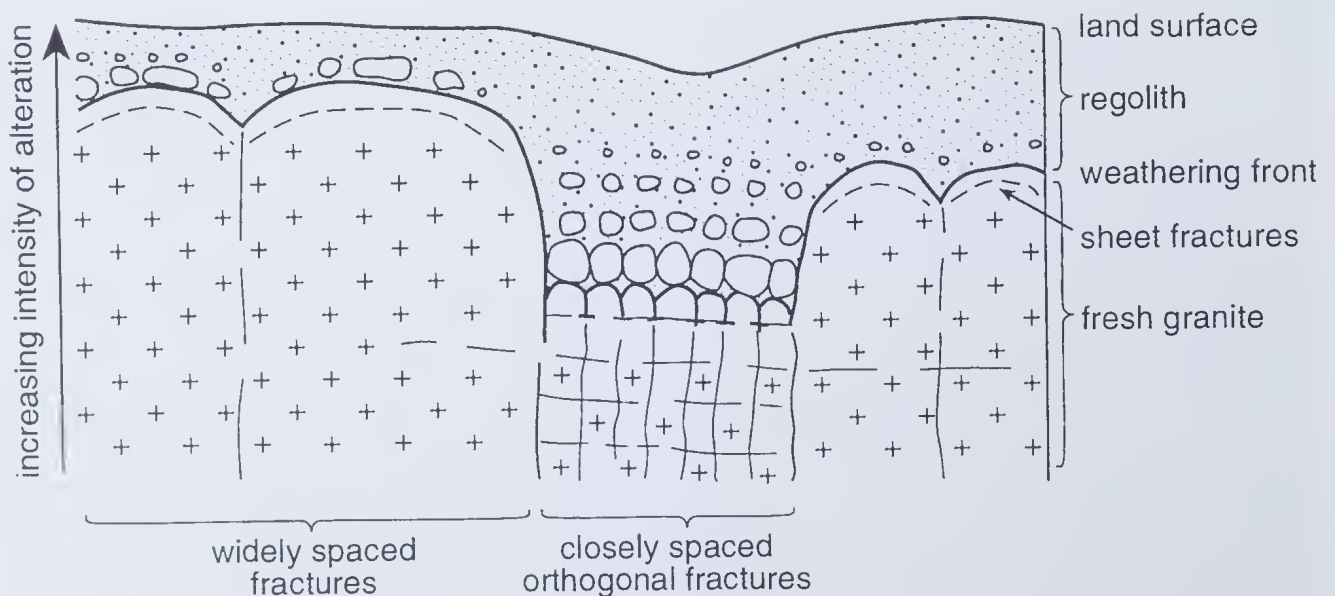


Figure 2. Schematic diagram illustrating the two-stage development of bornhardts. The subsurface exploitation of fractures by weathering is followed by the erosion of the regolith and the exposure of the weathering front. A similar two-stage or etch explanation of boulders is also illustrated (after Twidale 1982).

Major Landforms

Plains are well representative of granite outcrops; they take various forms. Peneplains are gently rolling surfaces, like those on northwest Eyre Peninsula, South Australia, and the southern Yilgarn of Western Australia. Pediments, or rock platforms, are smooth and gently sloping, essentially bare rock surfaces located on the margins of uplands. Mantled pediments carry an *in situ* regolithic veneer. Plains develop in different ways. Some are epigenetic, being formed by subaerial agencies, particularly running water. Etch forms, such as in the

plain around Meekatharra, Western Australia, develop as a result of weathering and the formation of a regular weathering front, followed by stripping of the regolith down to the weathering front. Some plains have been buried and later exhumed (Twidale 1982), like that resurrected from beneath a cover of Early Cretaceous strata, found in the north of Western Australia near Port Hedland.

However, it is the positive relief features that have attracted the attention of most geomorphologists. Twidale (1982, 1993) divided the major forms, on the



A



B

Figure 3. A: Flared slope on Ucontitchie Hill, Eyre Peninsula, South Australia. This prominent overhang is developed on a spur of massive rock, the shoulder of which is 5–6 m above the rock platform. The shoulder marks the level of the land surface prior to the stripping of the weathered material and exposure of the weathering front. B: Yarwondutta Rock, Eyre Peninsula, South Australia, showing flared side walls (S) and steps marking stages in exposure of the inselberg from beneath the regolith. The boulder with tafoni developed underneath is 2 m high. (CR Twidale).

basis of shape, into inselbergs, bornhardts, nubbins and castle koppies.

Inselbergs are isolated steep-sided island mountains rising abruptly from the adjoining plains (Fig 1). The forms also occur in groups or massifs. The shape of the individual hills varies. Bornhardts are the basic form. They are rounded, domical forms in massive bedrock, bounded by orthogonal fractures giving rise to a circular to square or rectangular plan shape. Sheet fractures, which parallel the surface, are prominent, resulting in a domical profile. Several explanations have been proposed for bornhardts. Some, *e.g.* the Pic Parana in south-eastern Brazil, are upfaulted blocks (Lamego 1938), but most are not fault-defined. Some granite bornhardts, *e.g.* those near Hiltaba in the Gawler Ranges, South Australia, are small plutons that have been exposed as a result of the preferential erosion of the weaker host rocks into which they were injected (Hurault 1963; Campbell & Twidale 1991), though such an explanation cannot apply to those bornhardts shaped in sedimentary rocks. In some instances, the composition of the bornhardts is more resistant to weathering than the rock of the adjacent areas (Hurault 1963; Brook 1978). However, most bornhardts are composed of

material of essentially the same composition as that underlying the surrounding plain.

Two explanations proposed to explain bornhardts have been widely accepted. First, bornhardts are considered by many to be the last surviving remnants following long distance scarp retreat (King 1942, 1962). If scarp retreat is a valid explanation, bornhardts ought to be restricted to major drainage divides but this is not so; backwearing of marginal scarps is restricted to a few score metres at most (Twidale & Bourne 1975a) rather than the scores of kilometres demanded by this hypothesis; and, if scarp retreat is involved, no bornhardt should survive through more than one cycle of erosion or, in general terms, for more than about 33 million years. Many are of greater antiquity and the upper parts of some on Eyre Peninsula, South Australia, may be of Mesozoic age, at least 100 million years (Twidale & Bourne 1975a). Also, the scarp retreat hypothesis is unable to explain several aspects of the field evidence (Twidale 1982).

Second, the field evidence points to bornhardts being structural forms developed on compartments of resistant rock with few open fractures whereas the surrounding rock is highly fractured and therefore subject to



Figure 4. A: Boulder-strewn surface of a granite nubbin, Naraku, northwest Queensland. Note the termite mounds in the foreground. B: Castle koppie, formed of angular joint blocks, near Harare, central Zimbabwe. (CR Twidale).

weathering (Fig 2). According to this theory, bornhardts develop in two stages; differential weathering beneath the surface followed by removal of the regolith to expose the weathering front. They are thus etch forms. The unfractured rocks are resistant to weathering and remain as high points in the landscape, whereas the well-fractured zones are easily weathered and are hence more susceptible to erosion. Once upstanding, bornhardts tend to shed water, which is concentrated in the lower zones where weathering proceeds more rapidly. In support of this hypothesis, numerous examples of convex-upward masses of unweathered granite have been exposed in excavations. Also, in many instances, for example at Ucontitchie Hill in South Australia, the fractures beneath the plain, and evidenced by dam construction, are closer than those widely-spaced fractures on the hill. In addition, the preservation of the outer layers of the bornhardt may be influenced by slight concentrations of iron oxide or silica associated with the weathering front; though lichens and mosses may also concentrate these elements after exposure (Twidale 1982).

The relative rates of weathering and erosion of the bedrock may lead to variations of slope of the exposed bornhardts. For example, flared slopes, as at Wave Rock, southwest Western Australia, and Ucontitchie Hill, Eyre Peninsula, South Australia (Fig 3A), and stepped topography (Fig 3B; Twidale 1982) are expressions of subsurface weathering and stages in exposure, as a consequence of which the bornhardts increase in relative relief as the surrounding plain is lowered.

Bornhardts are the basic major positive relief form from which nubbins and castle koppies are derived (Fig 4). The block- or boulder-strewn nubbins are due to the partial breakdown beneath the surface of sheet structures. Small, steep-sided castle koppies are explained as domes modified by pronounced marginal weathering along vertical fractures and in the subsurface. Alternatively, the presence of strongly-developed near-vertical fractures and pronounced frost action may result in the development of pointed or needle-like forms such as in the Organ Mountains in New Mexico (Seager 1981).

An etch origin similar to that for bornhardts but on a smaller scale is suggested for granite corestones and boulders, which are perhaps the most typical global granite form (Fig 4A). Spherical to ellipsoid corestones of intrinsically fresh rock are set in a matrix of weathered material. As the land surface is lowered the friable weathered material is removed leaving the boulders *in situ* (Hassenfratz 1791). This is the origin of such forms as the Devil's Marbles in central Australia (Twidale 1980). Pillars, such as Murphy Haystacks, Eyre Peninsula (Fig 5), are intermediate forms consisting of attached blocks or towers from which the surrounding regolith has been removed (Twidale & Campbell 1984).

Minor Forms

Minor forms developed on granite outcrops have been classified by Campbell & Twidale (1995b) into those due mainly to weathering and those that are tectonic in origin. Here this classification is generally maintained, although subdivisions are modified. Many of the forms have evolved in different ways *i.e.* they are convergent (Table 1).

In this brief review it is impossible to describe and explain each of these landforms. Rather a selected few will be discussed in order to illustrate the range of factors that are considered to be important in their development.

Rock basins

Rock basins, also known as gnammas, are circular, elliptical or irregular depressions in solid bedrock (Fig 6). Many are initiated at the weathering front which is demonstrated by the presence of shallow saucer-shaped depressions on recently exposed platforms. They commonly form along fractures and especially at fracture intersections. They are etch forms and after

Table 1

A classification of minor granite landforms. Those forms in *italics* are probably convergent.

1. WEATHERING FORMS

a. Initiated at the weathering front

Pitting
Flakes and spalls
Rock basins
Gutters and grooves
Polygonal cracks
 Flared slopes
 Scarpfoot depressions
 Deep indents
Caves
Clefts
 Pseudobedding
Blocks
Boulders

b. Due to partial exposure

Rock levées
 Rock doughnuts
 Fonts
 Pedestal rocks
 Plinths

c. Initiated at the surface

Rock basins
Gutters and grooves
Tafoni
Flakes and spalls
Blocks
Boulders

d. Due to crystal strain

Clefts
Gutters and grooves

e. Due to gravitational pressure

Rock basins
Tafoni

f. Due to intrusive veins

Clefts
 Walls

2. CONSTRUCTIONAL FORMS

Speleothems
 Boxwork pattern of ridges

3. TECTONIC FORMS

A-tents
 Blisters
 Triangular wedges
 Fault scarps
 Orthogonal cracks



Figure 5. Pillars of granite with flared side walls, Murphy Haystacks, Eyre Peninsula, South Australia (CR Twidale).

exposure develop varied morphologies according to the structure of the granite, the slope of the exposure and the depth of erosion. Flat-floored pans are the most common form, occurring on flattish crests in laminated rock (Fig 7). The laminations allow lateral weathering to outpace vertical weathering, in some cases resulting in overhanging sides. Hemispherical pits occur also on flattish crests but are developed where the granite is homogeneous, especially at depth beneath the superficial laminated zone. Armchair-shaped hollows are modified pans and pits and are restricted to steeper slopes. Cylindrical hollows develop where deep, concentrated weathering and erosion have extended a pit through a sheet allowing throughflow and abrasion of the form (Twidale & Corbin 1963; Twidale & Bourne 1978). On the other hand, some rock basins are formed on exposed surfaces. For instance, a basin formed on the crest of a menhir, or granite monument, at St Uzek, in Brittany, must have developed after exposure when the crest was placed in a roughly horizontal position about 5000 years ago (Lageat *et al.* 1994). Similarly, basins have formed on recently deglaciated surfaces as, for instance, in northern Portugal and southern Galicia (Vidal Romani 1989).

Gutters and grooves

Some gutters and grooves (horizontal Rillen and vertical flutings respectively) are initiated at the weathering front, for, like basins, they are developed on recently exposed bedrock surfaces, as for example at Dumonte Rock on Eyre Peninsula (Fig 8; Twidale & Bourne 1975b). Just as the saucer-shaped precursors of basins are shallow, so the gutters on newly exposed surfaces are shallow and narrow. Epigene gutters can be traced into the subsurface along the weathering front where they may converge and become shallower and wider, presumably as flow filtering between soil particles becomes diffuse, until they fade at a depth of several metres. Equally, however, and spectacularly at the menhir of St Uzek, grooves have formed on the exposed flanks of the erected slab (Lageat *et al.* 1994). Gutters

also are found on freshly deglaciated surfaces (Vidal Romani 1989). At Cash Hill, on Eyre Peninsula, gutters have developed on much of the exposed surface but do not extend beneath the regolith nor on the broad bench from which the regolith has apparently been recently stripped, suggesting that some gutters have formed subaerially.

After exposure, incipient gutters are enlarged by running water. Abrasion is evidenced by the development of potholes. In some cases the gutters have become flask-shaped in cross section as a result of the undercutting of side walls by streams and in part a reflection of their development in the laminated surface zone (Fig 9). Some gutters have exploited and follow fractures, but that slope is the prime determinant of the path followed by streams, and also gutters, is demonstrated by the many places where the gutters leave fractures to follow the steepest local slope. There are also instances, *e.g.* on Wudinna Hill, Eyre Peninsula, where elements of the drainage have migrated to new positions suggesting that fractures and slope are not the only factors influential in their development.

Gutters, in many instances, are developed along fractures but the fractures are not apparently present along the entire length of the landform and at some sites, *e.g.* Little Wudinna Hill, on Eyre Peninsula, gutters are paralleled by clefts in which no fractures are discernible; possibly the stresses responsible for fracturing affected the adjacent zones but were insufficient to cause rupture there (*cf* Russell 1935).

Gutters which descend from the summit of Yarwondutta Rock and The Dinosaur, both on Eyre Peninsula, South Australia, on reaching the overhang of the flared slope, bifurcate into two grooves on either side of a central rib (Fig 10). In an immediate sense this is apparently due to the protection afforded by a thin veneer of desiccated algal slime, but why the present channel floors are not similarly protected has not yet been explained.



A



B

Figure 6. A: Rock basin or gnamma, a hemispherical basin or pit developed on homogeneous granite, Pildappa Rock, Eyre Peninsula, South Australia. B: A 1 m deep pan developed in laminated granite and with overhanging sides, Yarwondutta Rock, Eyre Peninsula, South Australia (CR Twidale).

Flared slopes

Flared slopes are found in a variety of lithological, climatic and topographic settings. They are particularly well developed in the granite of south-western and southern Australia. Flares are characteristically found around the base of hills but they are also found on higher slopes (Fig 3A,B) and in clefts. Several distinct flares

may be present. Many flares are inclined rather than horizontal. On Eyre Peninsula, they are highest and best developed on the southern sides of the hills. Most significantly, flares shaped in bedrock have been exposed by excavation of the *in situ* regolith. Flared slopes evolve in two stages, the first involving subsurface weathering during which the hillslope is undermined. The tectonic

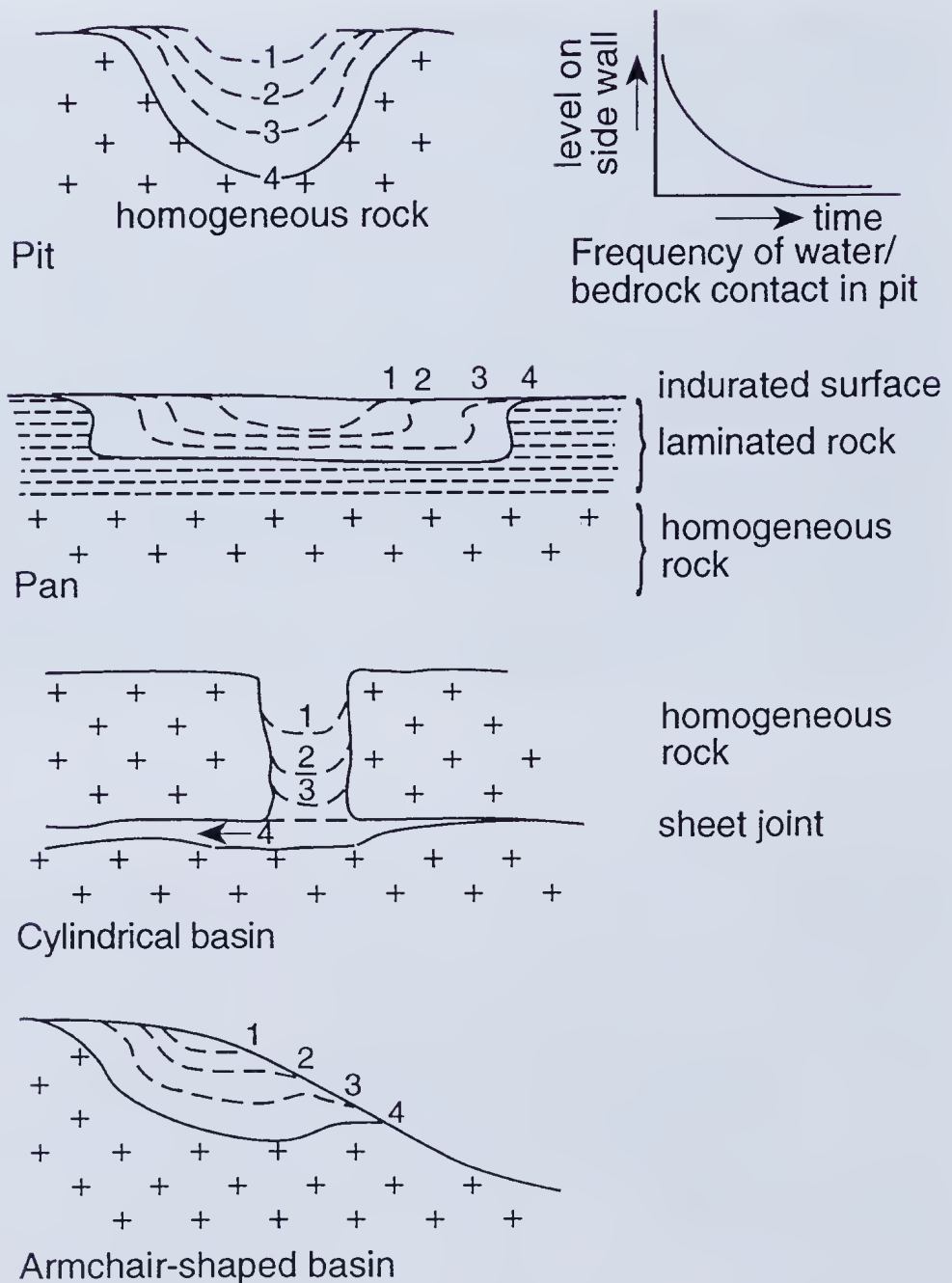


Figure 7. Schematic development of pits, pans, cylindrical gnammas and armchair shaped rock basins (After Twidale 1982).

stability of southern Australia has allowed time for intense scarp foot weathering to develop. The near surface zone dries out in summer, the dry season in southern Australia, but moisture and hence weathering persist at depth. The second stage involves the stripping of the regolith to expose the smooth, concave weathering front (Twidale & Campbell 1993).

Tafoni

Tafoni are hollows formed at the base of boulders and sheets and protected by an outer rim or visor (Fig 11). Some are associated with basal fretting or with flared slopes, suggesting that they too are initiated at the weathering front. Tafoni evolve as inverted saucers and

enlarge upward into the rock mass as a result of salt crystallisation, hence the occurrence of tafoni in arid and semiarid lands, in cold and arid Antarctica and also in some coastal areas. The preservation of the outer visor is an integral part of tafone development and is possibly due to concentrations of iron or silica. Tafoni are inevitably self destructive, for their very growth helps destroy the host mass in which they are located (Twidale 1982). They may also result from gravitational forces imposed by a large boulder resting on an outcrop and causing crystal strain at the point or points of contact, eventually leading to rock basins on the outcrop and tafoni on the underside of the boulder (Vidal Romani 1989, 1990).



Figure 8. Dumonte Rock, near Wudinna, Eyre Peninsula, South Australia. The regolith has recently been cleared to make a reservoir, and the former weathering front has been exposed. The gutters continue beneath the former soil level, X-X (CR Twidale).



Figure 9. Undercut side walls of gutters on Wudinna Hill, Eyre Peninsula, South Australia (CR Twidale).

Rock levées and rock doughnuts

Some minor forms are best explained in terms of the partial exposure of the bedrock surface. Rock levées are residual rims bordering shallow channels or gutters scored in bedrock. Rock doughnuts are annular rims encircling basins (Fig 12; Blank 1951a,b; Twidale & Bourne 1977). Protection by organisms and a coating of opaline silica (Whitlow & Shakesby 1988) have been suggested to account for their preservation. They can also be explained by the contrasted behaviour of wet and dry granite (Barton 1916; Twidale 1988). Little weathering takes place

in the seasonally dry regolith-free zones adjacent to the gutter or basin though weathering proceeds through all seasons beneath the regolith preserved over most of the surface.

Speleothems

Although the products of granite weathering form important components of sediments, constructional forms are rare in the granite context. Silica released by weathering is, in places, reprecipitated along fractures which are consequently sealed. After weathering of the



Figure 10. Inverted grooves on the flared basal slope of Yarwondutta Rock, Eyre Peninsula, South Australia. The gutters which drain from basins on the hill bifurcate at the top of the flared slope into two grooves. The central rib of each is covered with algal slime (CR Twidale).



Figure 11. Tafone developed beneath and within sheets 3 m thick at Ucontitchie Hill, Eyre Peninsula, South Australia (CR Twidale).



Figure 12. Rock doughnut, a raised rim encircling a small pan on Waddikee Rock, Eyre Peninsula, South Australia (CR Twidale).

surrounding granite, the silica forms a boxwork pattern of miniature ridges. In some areas silica from water seepages in open fractures is reprecipitated as small (up to 5 mm high) speleothems, most commonly in the form

of flowstone, stalagmites or stalactites (Caldcleugh 1829; Vidal Romani & Vilaplana 1984). The stems of the speleothems are composed of opal-A but, curiously, each has a tip of gypsum.



Figure 13. An arched slab of granite 15 cm thick with a crestal fracture and termed an A-tent, on Freeman Hill, western Eyre Peninsula, South Australia (CR Twidale).

A-tents

Tectonic processes are responsible for a small but notable suite of landforms in granite. A-tents, or pop-ups, (Fig 13) involve a permanent expansion, are consistently oriented in a given area and, in some instances as at Quarry Hill (Eyre Peninsula), have been induced by detonation of explosives. They have been attributed to insolation and to erosional unloading but their consistent orientation suggests they are best explained as associated with the release of compressive stress, in natural conditions probably in response to earth tremors (Twidale & Sved 1978).

Conclusion

Many of the landforms developed on granite, both major and minor, are related to the characteristics of the rock, the composition of the penetrating water, and the relative amounts of weathering and erosion. Depositional forms are rare. Tectonic factors are significant in a suite of forms due to the release of compressive stress.

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Granite outcrops: A collective ecosystem

B York Main

Department of Zoology, University of Western Australia,
Nedlands Western Australia 6907
email: bymain@cyllene.uwa.edu.au

Abstract

Ecological systems of granite outcrops are posed as having arisen through one of two processes or through a combination of both processes; through colonisation of exposed and weathered rock surfaces and/or through retention of components of relict biotic assemblages surrounding such exposures. In the context of such evolved ecological systems, the inter-relationships of outcrop configuration, the geological and climatic history and associated changes from mesophytic to sclerophyll or xeric vegetation of surrounding landscapes is discussed with reference to selected outcrops.

Introduction

Ecosystem, like biodiversity, is an "in" word. But what does it mean? As an abbreviation of ecological system, it denotes some sort of interaction of life forms and dependence within a physical, non-biological framework on which the living forms in turn have some effect. As a system, an inherent cohesion is intimated; external limits are inferred. All this in turn suggests that an ecosystem has boundaries. A dictionary supports this concept in the definition "*The plants and animals of a particular habitat, together with the environment influenced by their presence*" (Onions 1978). Ecosystems, as nominated in common biological parlance, can be large or small, relatively open or near-closed. An ecosystem can range from the complexity of a tropical rainforest to an individual tussock grass on Beauchene Island in the Falkland Islands archipelago (Smith & Prince 1984).

How then to define a granite outcrop ecosystem? It must comprise some sort of cohesive biotic community supported by a physiographic matrix, which embraces both time and space components and be clearly demarcated from any adjacent, contiguous or surrounding ecosystems. Granite outcrops were referred to early as monadnocks or "island hills" (Jutson 1934) who recognized them as exposed residuals surrounded by more readily weathered components of the underlying bedrock. They are currently regarded popularly as "islands" (Anon, undated). In the context of "islands" many botanical studies have been undertaken in southwestern Western Australia (Ornduff 1987). Current understanding and interpretation of the peculiarities of the biota of the outcrops has been partially wrapped in island biogeography theory. The obvious refugial role of the rocks has also been noted in relation to isolates of former more widespread and continuous distributions of plants such as jarrah (Abbott 1984) and also of various animals. Recognition of both the refugial and insular nature of granite outcrops has underpinned much of the drive and justification for conservation and

inclusion of particular rocks in the nature reserve system of Western Australia.

The "island" concept of outcrops has been generally stimulated by observation of their present biotic distinctiveness or biotic disjunction with their immediate surrounds, particularly in relation to vegetation and ephemeral aquatic fauna. While documentation of vegetation, vertebrates and aquatic invertebrates has already been undertaken on selected granite outcrops (see elsewhere in this issue), the terrestrial and/or lithic invertebrates are less well known. Few, if any, comprehensive studies have attempted to document the interactive relationships of the total biota of a granite outcrop although Main (1967) presented a simplistic naturalist's view of the ecology of a particular rock, Yorkrakine Rock, in the wheatbelt. McMillan & Pieroni (undated) have given a "primer" account of the life forms associated with granite outcrops.

To understand the representativeness and cohesion of the biota on any one outcrop and to be able to arrive at generalisations regarding the composition of the biota over the array of outcrops in any region or on a continental scale, I believe one needs to adopt an historical perspective. While documenting (a) the characteristics of the outcrops as they appear now and (b) the present biota, one needs at the same time to ask;

- How have these "ecosystems" come about?
- What were the antecedent landscapes like?
- How has the biota responded to the sequential changes of the landscapes through to the present time?

I shall now attempt to show that by adopting this historical approach we can come to some understanding of

- the physiography of the outcrops,
- the distribution and restriction of dominant elements of the biota,
- "ecosystems" of selected rock configurations, and
- over a geographic span suggest that there are biotic patterns peculiar to granite outcrops which comprise a "collective ecosystem".

From the outset, my discussion will be limited largely to the granite outcrops of southern Western Australia, south of approximately 26 degrees latitude, and hence those which occur in a predominantly winter rainfall region. In the more northern and eastern areas particularly, they are also affected by summer rainfall in the form of thunderstorms. Outcrops near the south coast experience the benefit of coastal precipitation either as light drizzle or fog induced by onshore winds associated with high pressure systems. The relevance of the overall discussion to outcrops elsewhere, particularly Eyre Peninsula, is implicit.

Distribution and Characteristics of Granite outcrops

The present scenario

Granite outcrops, as loosely defined, are scattered throughout southern Western Australia from north and west of the Nullarbor *i.e.* from the arid interior, through woodlands and forest country to the southwest coast. They appear as emergent protuberances of the basement rock over the Great Plateau or Archaean Shield (of the Yilgarn craton) and similarly as promontories on the dissected edges of the western escarpments and across the southern landforms of the state. Jutson (1934) referred to these "island hills" as remains of the "old plateau". Clarke (1994) dated the "stripping" of the regolith of much of the Yilgarn craton (which would account for "granite" exposures) as between Middle Jurassic and early Eocene and associated such stripping with uplift and incision of the palaeodrainage system. It is outside the scope of this paper to discuss the petrology or origin of the rocks which aspects are dealt with elsewhere in this issue. It is only relevant here to discuss the physiographic configurations of the rocks as they affect the biota and its distribution.

Widely scattered as they are, the rocks fall within three major rainfall zones as defined by Hopper (1979) as the high, transitional and arid rainfall zones representing 800-1400, 300-800 and less than 300 mm per annum. Interestingly, rocks within these three zones can be more or less defined by their grey, brown or red colour respectively which reflects indirectly the response of living organisms *e.g.* types of predominant lichen growths, or conversely their absence, to the rainfall gradient. The composition of the ecosystems of particular rocks is determined partly by the present rainfall *i.e.* the zones as delimited above, by the geo-climatic history with the associated changes from a mesophytic to sclerophyll and xeric vegetation and the configuration and topography of the rocks.

Configuration and topography of rocks

Configuration of rocks ranges from high, sharply declivous domes to barely perceptible, flat exposures. Such configurations generally reflect the degree of erosion of the surrounding landscape which in turn has exposed the basement rock to varying degrees. A convenient characterisation of the predominant configurations adopted here (Fig 1) is as follows:

- Single or multiple domes, monadnocks or tors, as "islands" on the dissected Darling Plateau and in a

landscape of low relief *e.g.* the predominant outcrops of the Great Plateau ("inselbergs" of Jutson (1934); Fairbridge & Finkl (1978); Finkl & Churchward (1974) and in part "bornhardts" of Campbell (1997).

- Flat, often disc-like pavements (Fig 1) which are also a frequent feature on the plateau.
- Subsurface basement highs, here referred to as "fugitive outcrops" (Fig 1).
- Asymmetric declivities or tors as exposures in mountain ranges *e.g.* the Porongurup Range and throughout the forested southwest of Western Australia (comparable to the domes of The Plateau).
- Coastal declivities and near-coastal knobs protruding through Pleistocene limestone deposits.
- Tumuli of boulders either around a central core or as rock "piles" (Fig 1; Plate 1). The latter are sometimes adjacent to salt lake lineages where they may be erosional features of former domes which have weathered to blocks in association with the presence of salt. Such rock piles are comparable in part to "nubbins" and "castle koppies" of Campbell (1997).
- Scattered boulders (especially on escarpments or ridges), or clusters of small tors, or "haystacks" (Twidale & Campbell 1984).

It is the domes (monadnocks or tors) and the disc-like pavements which most closely fit the general concept of an "outcrop" *i.e.* as a sizable, isolated "intrusion" into the landscape (Ornduff 1987) and it is predominantly these configurations which will form the main focus of my discussion with reference to others as listed above for comparison. However, all types of configurations share some basic ecological elements while differing in structural and biotic detail. A combination of rock topography, which has been partly determined by past erosion and climatic patterns, and impacts of current weather conditions determines the level of complexity of the ecosystem of a particular outcrop.

Topographic features and associated biota of outcrops

The more subdued the profile of an outcrop the less complex the topography hence a "pavement" rock generally presents little sculpturing whereas a higher exposure exhibits a more varied topography (Fig 1). The main topographic features of an outcrop are associated with the sculptured surface and the surrounding "apron".

The sculptured surface. The sculptured surface may be relatively "smooth" or pitted and dimpled (Jutson 1921). As well as the rock crust having partially detached pieces, including "pop-ups" or "A-tents" (see Campbell 1997), the surface may also be littered with exfoliated plates, flakes or slabs. Both attached and loose rock plates provide habitat for invertebrates *e.g.* spiders, centipedes, scorpions, pseudoscorpions, opiliones, pupating insects, moths, beetles and also vertebrates particularly frogs and lizards such as geckoes and the agamid *Ctenophorus ornatus*.

The wave-like slopes ("flared slopes" of Campbell 1997) of some higher domes have been variously interpreted as the result of subsurface weathering in the presence of water (see Campbell 1997) or partly by

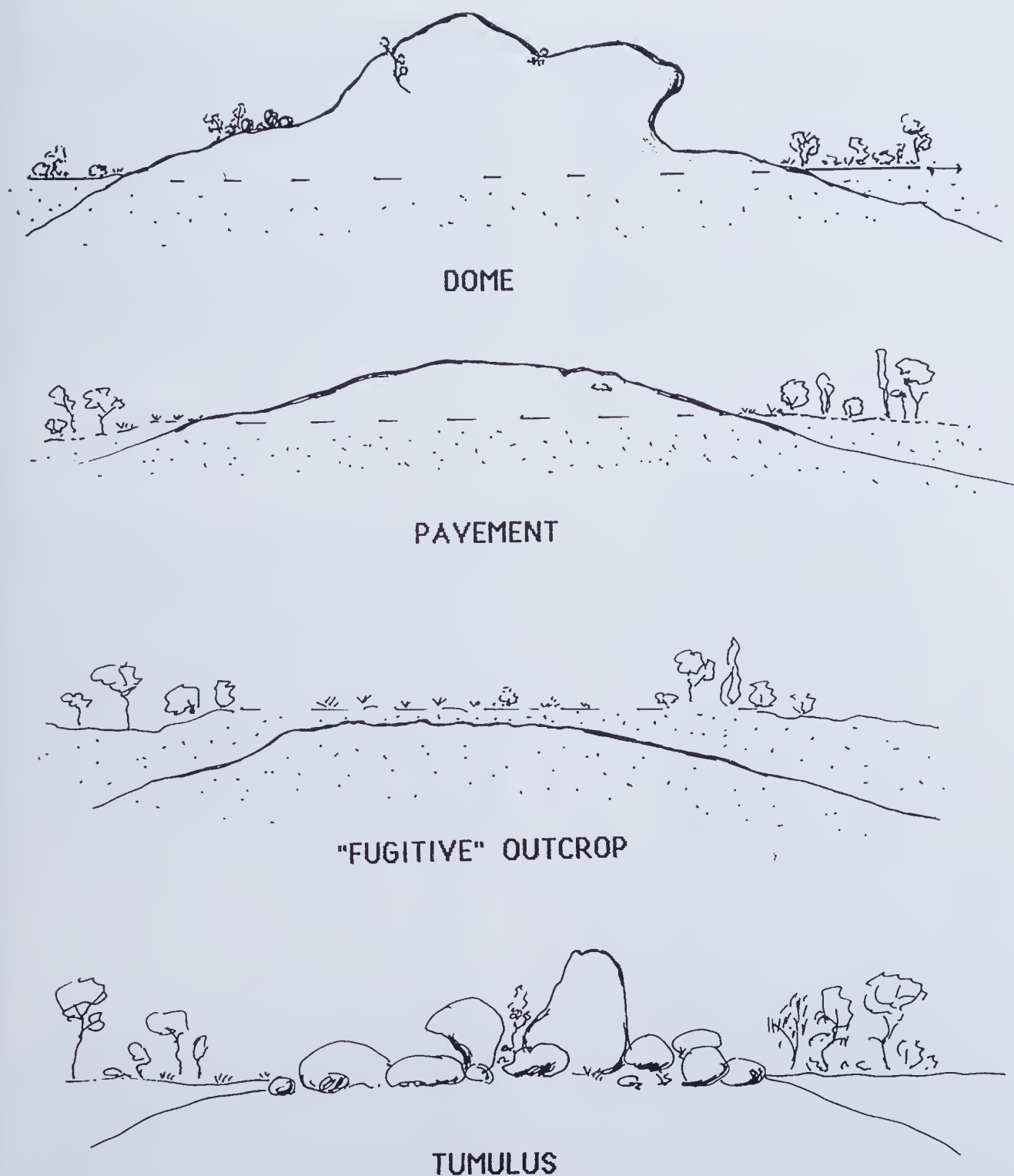


Figure 1. Examples of configurations and topography of granite outcrops.

sandblasting by wind. However some initial sculpturing may have been by the Permian ice sheet which is known to have covered much of southwestern Western Australia (McWhae *et al.* 1958). Earlier, Clarke (1919) had remarked on glacial deposits in inland southern Western Australia as have Fairbridge & Finkl (1978). However, Clarke (1994) doubts that any relicts of Permian landforms could be anything but minor and restricted today. The “waves” form dramatic drops and

frequently direct rain onto either surrounding aprons or into flat bottomed gorges from which creeks may debouch. Both such sites provide moisture-holding habitats.

Certain outcrops weather into block formations (Jutson 1934) and have large boulders both on their profiles and scattered around the base (see “nubbins” of Campbell 1997). These boulders sometimes erode into cave-like shells (tafoni) or narrow-based pedestal shapes

(see Campbell 1997). Runoff water from the boulders maintains a moister habitat than the general rock surface and where there are clusters of boulders, intervening soil supports ephemeral and perennial vegetation. The boulder piles or clusters (Plate 1) form habitats for animals ranging from invertebrates to vertebrates such as bats and marsupials (euros and rock wallabies) and snakes and varanid lizards.

"Fugitive" outcrops (Fig 1) of the basement rock often appear as open meadow-like spaces surrounded by higher shrubby vegetation, woodlands or forest. They are vegetated by the same fringe or meadow plants as occur on rocks in the same region. As summer-dry bogs they provide habitat for relict burrowing spiders *e.g.* the mygalomorph *Teyl* (Withers & Edward 1997, Fig 2) and various insects such as cicindellid beetles.

Algae and lichens occur on most rock surfaces. Lichens are renowned for being able to withstand extremes of temperature. Pertinent to growth and survival on granite outcrops is the fact that dry thalli of some genera have been demonstrated to resist temperatures as high as 70-101 °C. However, the tolerance of moist thalli does not exceed 46 °C (Lange cited by Hale 1967). Some lichens are very long lived but they are also colonisers *e.g.* *Parmelia* occurs abundantly on the rocks. Lichens have the capacity to fix nitrogen and in the presence of rain to leach minerals from the rock surface. In so doing, they gradually break down the rock surface forming soil particles. Thus their role in making granite outcrops suitable for colonisation by mosses and finally other plants is highly important (Plate 2). While no studies appear to have been conducted in southern Western Australia on the possible association of organisms such as invertebrates living in the thalli, certain moth larvae feed on lichens on the outcrops (*pers obs*).

In wet areas, considerable moss mats or swards occur where a little soil has accumulated. Larger rocks with higher profiles frequently have deep crevices which similarly support moss mats and rock ferns (the most common and widespread being *Cheilanthes*) and also the blind grass *Stypandra* and various shrubs *e.g.* *Baeckea*, *Beaufortia*, *Kunzea* or *Anthocercus* depending on the location. *Kunzea*, which is common on dryer rocks, characteristically also grows from deep narrow fissures and thus gives the appearance of hanging from the rock itself. In contrast *Anthocercus* which grows in higher rainfall areas grows in the moss mats or swards and consequently often suffers windthrow (Plate 3).

Higher rocks may also have shelves with an accumulation of soil where again moss mats, ferns and shrubs flourish. Newbey (1995) remarked on deposits of "skeletal soil" up to 30 cm deep on lowlying areas of granite exposures. These deposits may also provide habitat for perennial mygalomorph spiders. The interface of rock and soil of crevices and shelves is frequently fringed with the liliaceous pincushion plant *Borya* in dryer areas, and in wetter areas the heather-like *Andersonia*. *Borya*, as one of the "resurrection" plants (Gaff 1981) is able to withstand considerable desiccation during which times it assumes a striking orange colour (Plate 2), but reverts quickly to a bright green following water uptake after rain (see Plate 5, and Hopper *et al.* 1997). A variety of orchids, composites and other ephemerals intermix near these fringes. Various

invertebrates such as insects and spiders live in any soil accumulations *e.g.* of crevices and shelves, which support plant life. The gorges, in the higher rocks, support the same sort of vegetation as the shelves with occasionally the addition of the Christmas tree (*Nuytsia floribunda*), *Allocasuarina huegeliana* and *Acacia rostrata*.

Large depressions ("dimples" of Jutson 1921; and in part "flat-floored pans" of Campbell 1997) occur on most outcrops which have at least some relatively flat areas. After rain these depressions fill with water to form ephemeral pools. The quillwort *Isoetes* frequently forms a dense lawn on the floor of such ponds. An array of invertebrates including the crustaceans Conchostraca (shield shrimp *Triops*), Cladocera, Ostracoda, Anostraca (brine shrimp), insect larvae, water mites, flat worms (Platyhelminthes), rotifers and also frog tadpoles are active seasonally in the ponds.

Rocks with higher topography encourage a cascading effect of runoff after rain. This runoff may erode the rock surface into tiers of pit-like depressions ("dimples"), of which the deeper ones are sometimes called "arm-chair basins", along drainage lines thus forming temporary waterfalls (Jutson 1921) which leave in their wake a series of longer lasting pools. A later seral stage of such stepped pools or water holes are soil-filled pockets which finally develop into "Babylonian gardens" (Plate 4).

Gnammas (rock holes) may be present on both dome and pavement configurations and are frequently permanent water reservoirs. As well as habitat for invertebrates, the pools and gnammas are an important source of water for vertebrates, both permanent habitat associates and transitory fauna *e.g.* birds and also bats (R How, *pers comm*; Dell & How 1984, p 69) and larger marsupials.

The meadows, formed over infilled ephemeral ponds, are a common feature on outcrops (Plate 5). Depending on the seral stage these are crusted with lichens or vegetated by moss mats, *Borya* or *Andersonia* heaths, blind grass and restionaceous tussocks and small shrubs such as may also occur on shelves or in crevices of the outcrop. In that these meadows form seasonal bogs, usually in winter but also during summer thunderstorms, they provide important habitats for moisture dependent organisms particularly invertebrates including species of the mygalomorph spider *Teyl*.

Fissures, crevices, shelf meadows and seral-pond meadows, boulder shadows where soil accumulates, lichen and moss around the lips of fixed rock plates, and even the soil spill around exfoliated slabs, all form to some degree relatively moist habitats when compared to the general rock surface. As such they form the principal habitats for smaller organisms, both invertebrates and vertebrates including frogs and lizards, while wallabies take advantage of larger boulder accumulations.

The apron. The descending edges of outcrops frequently fan out into soil covered aprons of varying width depending on the declivity of the rock. Soil depth varies from 1.5 to 2.0 m (Newbey 1984 p33, 1988 p11) and throughout the seasons are alternately waterlogged and dry, thereby constraining both the vegetation and soil living invertebrates. Shallow soils with little vegetation apart from moss mats and rock fern, and meadows of *Borya* and ephemerals or in wetter areas



Plate 1. A rock pile (tumulus) near Hyden, Western Australia, with surrounding *Allocasuarina* grove.



Plate 2. A meadow of *Borya* at edge of rock with adjacent lichen crusts on rock, Plover Rock, Western Australia. Note the "drought" mode of the brightly coloured *Borya*.



Plate 3. Wind-thrown *Anthocercus* plant on Torbay Hill, Western Australia.



Plate 4. "Babylonian Gardens" growing in the pockets of soil formed in the tiers of infilled rock holes (armchair basins) on Torbay Hill, Western Australia. This stepped sequence of soil pockets would formerly have been a seasonal waterfall.



Plate 5. A tiny *Borya* meadow formed in an infilled rock pool on a rock at Payne's Find, Western Australia. Such meadows provide habitat for the mygalomorph spider *Teyl* and other invertebrates.



Plate 6. The stem-flowering ("cauliflory") of *Hakea petiolaris*, a condition possibly relictual from an earlier climatic period when the plants grew under a canopy.

Andersonia, gradually blend into tussock and shrub thickets similar to the vegetation of the larger meadows and shelves on the rock proper or in the shallow gorges with the addition of sandal wood. In the semi-arid and arid region, the aprons may have an extension of indigenous grasses from park-like acacia groves. *Allocasuarina* shrubs and trees frequently fringe the outer extension of aprons or grow along creeks at the interface of rock edge and apron. Particularly on higher rocks which provide much runoff, the creeks at either the boundary of the apron or where they transect the apron are important seasonal habitats for invertebrates and frogs and in summer provide damp refuge areas. The apron meadows, like the meadows formed in infilled ponds and over "fugitive" outcrops, are sanctuary to relict burrowing spiders e.g. *Teyl* species which aestivate in sealed burrows, and insects whose larvae are dependent on a seasonally wet substrate.

Microclimate of outcrops and effects on biota

Outcrops, particularly in the semiarid and arid regions are subject to extremes of temperature and alternatively wet and dry seasonal conditions. Botanical studies and zoological works have both noted upper rock surface temperatures of over 50 °C (Marchant 1973; Bradshaw & Main, 1968). Bradshaw & Main (1968) also noted that air temperatures were at least ten degrees lower under the overhangs of attached rock plates and even under loose slabs. Animals such as the common ornate dragon lizard, *Ctenophorus ornatus*, take advantage of these retreats and also the shade cast by boulders. The latter also provide refuge from the heat for rock wallabies and euros. Presumably the large goannas also benefit from boulders and large semi-attached rock sheets.

Rocks and rock slopes of coastal hills, the southern mountains and southwest peaks e.g. Porongorups, Granite Peak, Mt Lindsay, Many Peaks and peaks in the Darling Ranges such as Mt Cooke, all benefit from the altitudinal self-generated cloud and fog mantles which increase the moisture content of vegetation, litter and soil thus providing microhabitats for invertebrates.

Conversely many rocks in regions of low rainfall while capturing isolated fog nevertheless do harvest moisture and thereby provide refuge for moisture dependent biota. It has been noted that even light rain generates run off from rocks. In winter 5 points (1.8 mm) of rain, in summer 7 to 9 points (2.5-3.2 mm) generates run off. More significantly it is recorded that "Kondinin Rock has been known to yield water from a light mist" (Ferne 1930). Such harvested water naturally channels into creeks at the rock/apron interface, around the base of boulders and into crevices and fissures and under overhangs and exfoliated slabs. It is also sufficient to wet dried beds of ponds and activate dormant insects and aestivating frogs. Thus, even minimal moisture catchment becomes of major importance for the survival of relict invertebrates.

Origin and Distribution of the Biota

Historical perspective and persistence

The outcrops appear as present day intrusions in the

surrounding landscape (Ornduff 1987) but they would not in earlier geoclimatic periods have stood out in such isolation. Although their lithic core would have set them apart topographically, a much wetter climate and mesophytic vegetation containing southern rainforest elements including *Nothofagus* and associated plants (Balme & Churchill 1959) would have maintained more continuity in the vegetation and fauna. Biotic isolation focused around granite outcrops would have begun in the Tertiary along with the sclerophylly of the vegetation. Outlying botanical components of the forest region of southwestern Western Australia associated with granite outcrops in the dryer transitional rainfall zone, such as the jarrah (*Eucalyptus marginata*) stand at Jilakin Rock (Abbott 1984; Churchill 1968) indicate the contraction of species to refuges in the face of changing climatic conditions. Another possible relict of an earlier bioclimatic scenario is *Hakea petiolaris*. This species exhibits the peculiar habit of stem-flowering or "cauliflory" (Plate 6), which White (1986) describes as characteristic of certain plants growing under a closed canopy. Thus it is possible that *H. petiolaris* is a relict of an earlier, wetter, forested landscape.

With a continued trend towards a dryer, more seasonal climate, invertebrates dependent on a continuously moist habitat would have become concentrated in microhabitats such as already noted around granite rocks, while many (as with larger vertebrates) may have disappeared altogether. Some animals show definite adaptive responses through life history strategies to increased aridity and marked seasonal changes by retreating to permanently moist microhabitats at certain times of the year. Others, such as the aquatic invertebrates (Crustacea, insect larvae, platyhelminths, etc) are well suited through dormant life history stages to avoid severe summer drought. For example, many branchiopod crustaceans have resistant eggs and can remain viable in the dry soil of ponds for long periods.

There appear to be few animals tied completely to rock habitats throughout their entire life cycle. The rock wallaby, although dependent for shelter on rocks, is more widespread and forages away from rocks. In some places euros similarly make use of rocks for shelter. Many other vertebrates such as kangaroos, echidnas, bats and a whole suite of birds make transitory use of granite outcrops especially as a water source and thus are probably dependent on them during summer drought but are not confined to them. Many frogs live and breed around rocks, but are not solely restricted to granite outcrops as a habitat.

A notable vertebrate which is confined to granite outcrops is the widespread dragon lizard, *Ctenophorus ornatus*, which thus represents a collective of disjunct populations. Similarly a few plant species have a fragmented distribution with occurrences confined to granite rock habitats e.g. *Isotoma* (James 1982), *Eucalyptus caesia* (see Hopper *et al.* 1982), *E. crucis* (see Brooker & Kleinig 1990), *Kunzea pulchella*, and some orchids. Certain invertebrates likewise are tied to granite outcrops. The biogeographically-ancient midge *Archaeochlus*, whose larvae develop in seeps on granite rocks, is an example (Cranston *et al.* 1987). Nevertheless, over the range of the genus in southwestern Australia and extending to Central Australia (P Cranston, *pers comm*) three species are

included. Most branchiopod crustaceans of the ephemeral rock pools occur on scattered outcrops. A well known example is the shield shrimp *Triops* which occurs not only on rocks but also along the edges of lakes and in temporary puddles in lowlying areas; there is no site specificity because of the wind-borne dispersal of the resistant eggs throughout the dry inland. The same probably holds for most aquatic invertebrates, except possibly for some water mites particularly in the forested south-west.

Various insects such as lichen-eating moth larvae and possibly some of the moisture-loving grasshoppers are possibly restricted to granite outcrops.

Amongst spiders, a *Rebilus* species (family Trochanteridae) occurs on many inland rocks where it lives under loose and attached slabs. Some other spiders with similarly flattened body form such as an unnamed lycosid, previously attributed to *Pardosa* (Main 1976, Plate 25) is confined to inland granite rocks while *Hemicloea* species occur under slabs on granites in southern forest areas but it is doubtful whether it or *Rebilus* are confined to rock habitats. *Selenops*, although a rock inhabiting genus, is not restricted to granite but is found also on sandstone formations. Other spiders frequently found on granites include wolf spiders such as *Lycosa leuckhartii*, *Miturga* species and the redback spider *Latrodectus hasselti*. All are readily dispersed and not confined to granites.

Site specificity

In contrast to this pattern, an interesting mygalomorph spider genus, *Teyl*, which is widespread in south-west Western Australia (and occurs in restricted areas of Eyre Peninsula and western Victoria), appears to be one of the few genera of animals which has at least some species restricted to particular granite outcrops *i.e.* species that are site specific. A striking confirmatory example is an undescribed species from Paynes Find Rock in which the spider exhibits an aberrant carapace modification (an everted fovea). This peculiarity does not occur in species of neighbouring rocks and indicates development of a morphological feature in isolation. The spiders are extremely sedentary, do not readily disperse and are active for only a very short period of the year. The spiders live in burrows in the meadows (Plates 2 & 5) and apron soils of the rocks and seal the burrows when the soil begins to dry out. At least one species of pseudoscorpion *Synsphyronus elegans*, which lives under rock slabs, appears to be site-specific to Yorkrakine Rock (north of Tammin).

While there are few data on either endemism to granite outcrops and/or rock-site specificity of invertebrates there is apparently considerable botanical endemism of particular rocks (see Hopper *et al.* 1997). The lack of invertebrate data may be giving a false impression of low endemism.

Biogeographic patterns: relative ages

Those invertebrate species which are confined to particular rocks probably indicate an older biogeographic phenomenon than those species which have not speciated in response to habitat isolation. I suggest this speciation began with the change to sclerophylly and seasonality in the early and mid-tertiary which would have induced a

concentration of moisture loving organisms around the granite rocks, not because of any special affinity for rocks *per se* but because of their capacity to provide wet microhabitats in an otherwise dry terrain. This moisture holding capacity of areas around substantial granite outcrops also holds good for "fugitive rocks". Main (1996) noted the occurrence of Mesozoic genera of mygalomorphs such as *Teyl* in microhabitats over granitic "basement highs" on relictual parts of the old Tertiary plateau of the wheatbelt of southern Western Australia. The model she presented could explain the distribution of many archaic invertebrates associated with higher parts of the inland plateau which in turn embraces many granite outcrops.

A richer fauna of both vertebrates and invertebrates must have existed during the mid-to-late Tertiary and into the Pleistocene, similarly focused around granite outcrops, but some of which has become extinct along with increased aridity. Fossil deposits of diprotodonts and other vertebrates at Balladonia (Glauert 1912) from a dam excavation adjacent to granite domes indicates just such a concentration (even if only seasonal) as we now see for certain extant organisms. Such species may also have been associated with other granite rocks which did not provide the same extensive boggy conditions suitable for fossilisation.

At best, the granite outcrops currently preserve a partially relictual, but also a predominantly widespread although contracted and fragmented biota. Nevertheless, high botanical endemism has been demonstrated for selected taxa which have been extensively studied. This suggests that the invertebrate fauna requires comparable in depth surveys, particularly of those forms with sedentary behaviour.

Aeolian reinforcement

The role of lichens and algae in both physically breaking down a "sterile" rock surface and also "capturing" atmospheric nutrients, primarily nitrogen, and thereby making a substrate or creating an environment for other organisms, has already been noted. An additional primary and continuous source of biological enhancement of granite outcrops is prevalent in what may be termed the aeolian medium. Swan (1992) defined an "aeolian zone" as "a region around and beyond the limits of the flowering plants". He suggested that the combined aeolian zones of the world constitute an "aeolian biome". An expanded definition of the "aeolian biome" could readily embrace granite outcrops both during the initial stages of their colonisation and later, even when a considerable associated biota has developed. The isolated granite outcrops of south-western Western Australia and/or other parts of southern Australia provide staging posts or scattered points in a biological lattice. Aerially-borne nutrients, and organic and inert debris as well as propagules of plants and animals (as spores, seeds and resistant eggs, and various other life history stages of invertebrates, including Collembola, aphids, thrips and large-winged insects) all combine to provide a continuous aeolian reinforcement of spatially isolated granite outcrops.

The seasonal behaviour and dormancy of some of the invertebrate fauna has already been mentioned. Spiders

NEEDS OF BIOTA IN USE OF GRANITE ROCKS

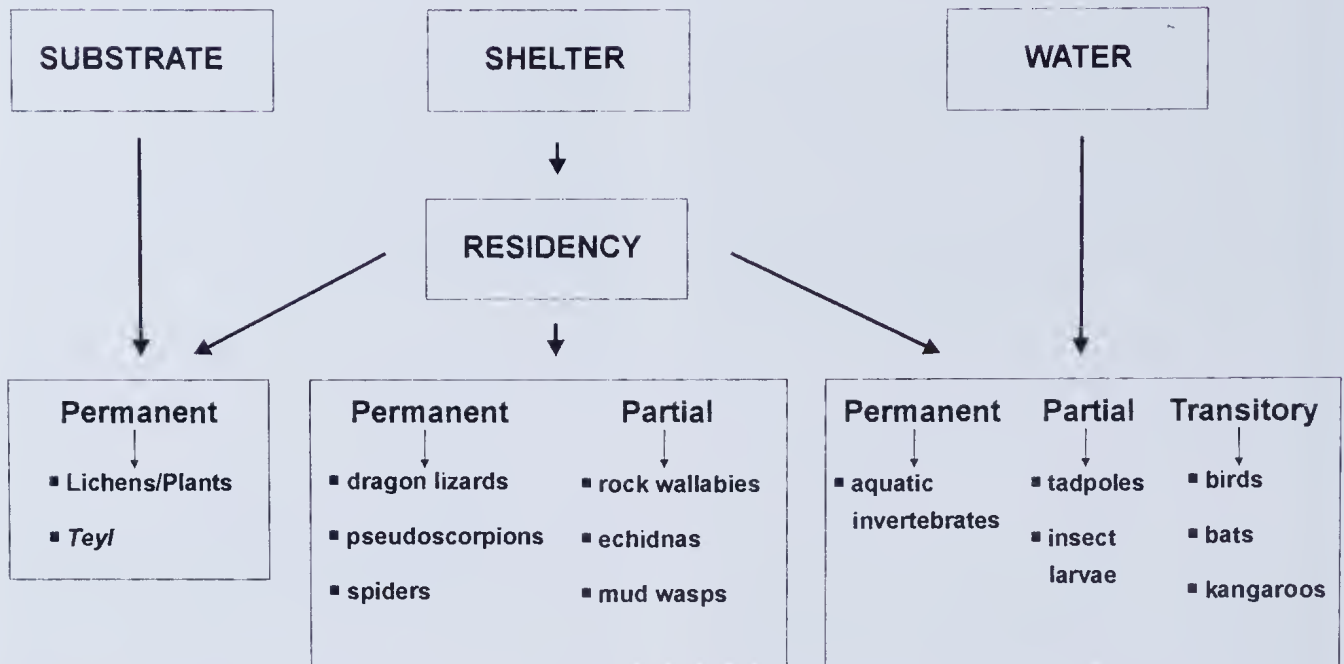


Figure 2. Selected examples illustrating the needs of the biota in their use of granite outcrops summarised according to their residency status in relation to provision by rocks of a substrate, shelter and water. Amongst the transitory fauna dependent on rocks for water, the present environment includes feral animals from rabbits and foxes to camels and donkeys.

such as the poor disperser *Teyl* are dormant for at least six months of the year secluded in sealed burrows, but other organisms deposit eggs or encysted dormant stages in the soil or dried out beds of ephemeral ponds. These latter organisms may be dispersed aerially, hence both reinforcing otherwise isolated populations and inhibiting allopatric speciation. Not only are propagules of plants and invertebrates aerially dispersed but also adult insects may form part of the aeolian fauna thereby accounting for the general lack of rock specificity.

Irregular but recurrent weather events such as cyclonic winds, tornadoes, dust storms and local "cock-eyed bobs" (Hunt 1929) each with their propensity for lifting, distributing and dumping fine biotic material, all reinforce the aeolian element of granite rocks.

Thus, finally, although from present knowledge the biota (especially of the fauna) associated with granite outcrops appears to have a distinctiveness, it represents predominantly a collective of "refugees" rather than an array of separate biotas tied to particular sites. Nevertheless I believe the relict mygalomorph genus *Teyl* may be representative of many other invertebrates of which we are not aware. This example indicates the need for thorough comprehensive surveys of invertebrates on selected outcrops over a wide geographic range.

Geographic replacements

In spite of the taxonomic commonality over a wide range of rocks, especially at the generic level and in many cases the lack of species endemism, there are some noticeable geographic replacements by ecological "equivalents" of certain rock adapted organisms, both

plants and animals, or organisms centred around outcrops. For example *Anthocercus* of the southern forests is replaced by *Kunzea pulchella* in the wheatbelt, which in turn is replaced by a *Beaufortia* in the eastern Goldfields. Amongst spiders over the same geographic span, *Hemicloea* is replaced by *Rebilus* and a lycosid. Trapdoor spiders of the Aganippini similarly replace one another in the apron meadows and fringing vegetation of disjunct rocks. Although superficially such replacements may be loosely regarded as "equivalents", a better term might be "behavioural counterparts" since the replacements are clearly associated with the rainfall zones and as such, physiological and interactive differences must be associated with the taxonomic shifts.

Further study of this phenomenon as demonstrated by a selection of taxa over a geographic span of rocks could well prove worthwhile.

Conclusions

The ecology of the biota can be summed up in the concept of the needs of the respective taxa in relation to what the rocks offer towards their livelihood (see Fig 2). The use of granite outcrops in satisfying the needs of their resident biota are primarily related to the functions offered by (a) the substrate *i.e.* the rock surface as a "home base" or attachment plane, (b) the rocks as shelter, and (c) the rocks as a water source. The biota can be grouped into permanent, partial or transitory residents according to the degree of association throughout the organisms' life histories.

No one rock maintains a "closed" ecosystem. Although some rocks with complex configurations and diverse biota with a high degree of interaction as measured by botanic richness, habitat availability for fauna, and food chains, may tend towards self-containment they are in fact still "open" in the same sense that a cave ecosystem is. Cave ecosystems are dependent on residents (such as bats) which live partly outside the cave to bring in some nutrients and also on the accidental deposition, such as by floods, of detrital matter. Granite rocks similarly are dependent on the partial and transitory residents to enrich the ecosystem. In addition the propagules and non-biotic detritus supplied by the aeolian medium continuously enhance the viability of a rock ecosystem. Thus even those elements which have permanent residency have some dependence beyond the margins or physical boundaries demarcating a particular rock. Figure 2 summarises the relationship of a granite outcrop biota to the outcrop and the surrounding environment.

In essence it can be stated that granite outcrops support a characteristic assemblage of plants and animals comprised of isolated populations of relictual genera and/or species, and widespread examples from the surrounding environment. There are many examples of granite outcrops, as isolates, retaining components of a once more widely distributed biota, for example the stand of jarrah trees at Jilakin Rock (Abbott 1984). With increasing sclerophylly of the vegetation associated with a drying of the climate since the mid-late Tertiary, the granite outcrops because of their water harvesting/retention capacity have become the foci around which moisture-dependent organisms have concentrated. Nevertheless they support both sedentary isolates and mobile, wide ranging organisms as well as wind-borne biota.

It is notable that apart from the more sedentary organisms and particularly elements of an older evolutionary radiation, such as the Mesozoic mygalomorph spider genus *Teyl*, most animal genera have not speciated in association with particular outcrops in spite of population fragmentation. Few organisms are endemic to particular rocks. However, there is evidence that there is a high level of genetic difference between populations of particular species from different rocks. Endemicity *i.e.* rock-specificity amongst plants, appears to be more pronounced, on present evidence, than amongst the fauna. In contrast to the taxonomic conservatism of much of the outcrop biota there are some interesting examples of geographic replacement of behavioural counterparts represented by unrelated taxa particularly over the rainfall gradient.

Also of interest, many organisms although now confined to granite outcrops either entirely or for a greater part of their life history do not exhibit adaptations peculiar to "rock-living" (the agamid lizard *Ctenophorus ornatus* and certain spiders *e.g.* a lycosid are exceptions) but rather are confined now to rocks because of their refugial role in maintaining cool, moist habitats on which such species are dependent as a legacy from their earlier historical environmental association.

In summary, a granite outcrop at the individual level maintains a co-operative of refugees, but on a broad scale granite outcrops represent a collective ecosystem.

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Reproductive ecology of granite outcrop plants from the south-eastern United States

R Wyatt

Institute of Ecology, University of Georgia, Athens, Georgia 30602 USA
email: wyatt@dogwood.botany.uga.edu

Abstract

Most of the Piedmont Physiographic Province of the southeastern United States is covered with mixed mesophytic forest of oaks, hickories, and pines. Within this "sea", however, are "islands" of exposed granite and gneiss. A characteristic, and largely endemic, assemblage of plants has adapted to the environmental extremes that bare rock provides by strongly altering their morphology, physiology, and life history. With respect to their reproductive ecology, however, these plants appear very similar to their congeners and to the Piedmont flora as a whole. Except for ant-pollinated *Diamorpha smallii*, most species show the expected range of pollen vectors, including wind, bees, flies, butterflies, moths and one species of hummingbird. Fruit and/or seed dispersal appears to be highly localised and effected primarily by wind and water. If anything, most species appear to possess adaptations against long-distance dispersal, which would carry propagules into the inhospitable matrix of oak-hickory-pine forest. Mating systems are variable, including examples of both self-compatible and self-incompatible taxa. Consistent with the expectation of low gene flow between populations on isolated outcrops, genetic data show strong differentiation and suggest the potential for genetic drift and/or natural selection to result in divergence. Some of the endemic species on granite outcrops have originated by allopolyploidy, whereas others appear to represent products of more gradual divergence in geographical isolation. There is reason to believe that some weedy species of early successful sites were originally restricted to granite outcrops and spread more recently to sites disturbed by human activities.

Introduction and Background

Most of the Piedmont Physiographic Province of the southeastern United States is covered with mixed mesophytic forest of oaks, hickories, and pines. Within this "sea", however, are "islands" of exposed granite and gneiss. Such areas constitute a habitat archipelago, supporting a largely endemic assemblage of plants and animals that are remarkably well-adapted to the environmental extremes that bare rock provides. These outcrops are known locally as "flat rocks" or "cedar rocks" and differ strikingly in vegetation from the surrounding Piedmont forest (McVaugh 1943). They occur from central Alabama to south-central Virginia and range from flat exposures of a few square metres to steeply sloping domes 200 m above base level that cover hundreds of hectares (Quarterman *et al.* 1993).

Originally, biologists speculated that the granite outcrops were of relatively recent origin, their appearance having been initiated through burning by native Americans and hastened by the erosion that accompanied poor lumbering and farming practices of European settlers (*e.g.* Oosting & Anderson 1939). Geological evidence, however, indicates that these rock units are >350 10⁶ years old and that the occurrence of exposed rock in the Piedmont probably dates back at least 150 mybp. This molten, igneous rock was intruded into pre-existing country rock and has become exposed in places where the erosional

cycle of the Piedmont has weathered away surrounding rock that proved less resistant (McVaugh 1943). Individual rock outcrops may, therefore, be much younger than might be suggested by the presumption of their existence 150 mybp. The endemic plants and animals have probably "island-hopped" from exposure to exposure as local erosional forces created new outcrops and covered older ones (Wyatt & Fowler 1977).

Weathering of the granite itself produces distinctive patterns and creates special habitats to which plants have adapted (Burbanck & Platt 1964). Uneven weathering of the surface produces rock-rimmed depressions that retain water between sporadic rainstorms in the late winter to early spring. These weathering pits may later become filled with sand and organic debris. Invasion of these depressions by plants speeds the chemical weathering process, as rainwater combines with CO₂ from the plants to produce carbonic acid. On domed outcrops, exfoliation occurs regularly. Huge shells of rock fracture and slide over the top of underlying layers, exposing fresh granite and creating talus at the base of the dome.

Environmental conditions on granite outcrops are harsh and differ sharply from conditions in the adjacent forest. Temperatures on the outcrops typically are much higher than in the forest because of high incident radiation, absorption of heat by the rock, and low evapotranspiration. Temperatures in excess of 50 °C are common at the rock surface during summer months. Moreover, the shallow, mineral soil overlying impervious rock and the low vegetation cover lead to extraordinarily high runoff. It is estimated that >95% of the annual

precipitation in outcrop communities is lost as direct runoff versus only 10%, on average, for the Piedmont of Georgia (Duke & Crossley 1975). These characteristics of granite outcrops, despite their location within a region that receives >1200 mm of annual precipitation, make them islands of desert embedded in a sea of mesic deciduous forest.

The decidedly desertic nature of the outcrops is reflected in the morphological, physiological, and life-history adaptations of the characteristic plants. A number of perennial species tolerate the extremely hot, dry conditions by storing water in succulent stems or leaves (e.g. *Opuntia humifusa*, *Talinum teretifolium*, *Portulaca smallii*). Others use CAM (Crassulacean Acid Metabolism), a photosynthetic pathway that enables them to use water very efficiently. By day, their stomata are closed as they store light energy in the form of organic acids. At night, their stomata open to take in CO₂ to be fixed into carbohydrates. Water loss by transpiration through open stomata is therefore minimised in such species as *Diamorpha smallii* and *Sedum pusillum*.

Perhaps the most widespread solution to the desert conditions, however, is drought avoidance. The overall abundance of different life-forms (*sensu* Raunkiaer 1934) shows a much lower proportion of trees and shrubs and a much higher proportion of annual herbs than are found in Piedmont forest (Phillips 1982; Walters & Wyatt 1982). In particular, the winter annual life history is extremely common among the characteristic plants of the granite outcrops. Seeds germinate after late September or early October rains to produce a rosette of frost-resistant leaves. When temperatures start to rise in late March or early April, the plants bolt and flower profusely. By early May, when the shallow soil depressions have become bone-dry, these winter annuals have matured a new crop of seeds, which require an after-ripening period of 4–5 months. Thus, they are able to survive the extremely hot, dry summer months as dormant populations of drought-resistant seeds. In addition to *D. smallii* and *S. pusillum*, there are many winter annuals, some of which, like *Agrostis eliottiana*, are the only annual members of groups that are typically perennial. *Arenaria glabra*, which is sometimes treated as merely a variety of the arctic-alpine perennial *A. groenlandica* (e.g. Radford *et al.* 1964), differs chiefly in its annual life history, whose evolution presumably enabled the species to invade granite outcrops.

Predictions

We have, then, a situation on the granite outcrops of the southeastern US that should permit us to make certain predictions about the reproductive ecology of the characteristic plants.

1. The evolution of the characteristic, and largely endemic, outcrop flora will be paralleled by the evolution of the pollinating and dispersing fauna.
2. Because of their importance to colonising ability, self-compatibility and self-pollination will commonly evolve (Baker 1955).
3. As is often seen in island floras, there will be secondary losses of dispersibility and the evolution of dioecy (Carlquist 1974).

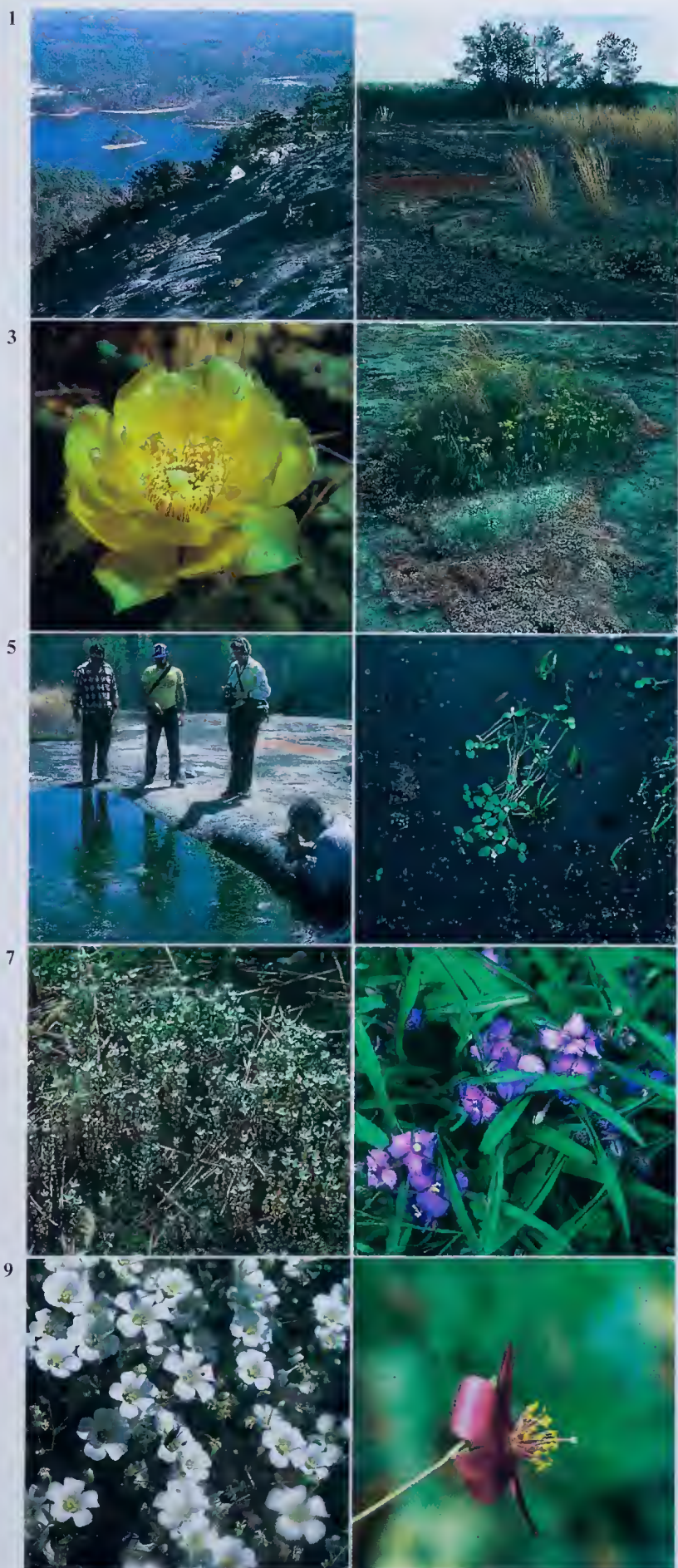
4. Population-level genetic differentiation among populations will be strong.
5. Speciation in these small, peripheral isolates will occur rapidly via allopolyploidy or other saltational mechanisms.
6. Because outcrops provide open, relatively low-competition habitats, many weedy species will be able to invade outcrop communities.

Empirical Evidence: Patterns and Processes

Despite the evolution of a number of animals that are endemic to granite outcrops (Quarterman *et al.* 1993), none of these serve as important vectors for pollen or seed dispersal. The activities of most, like the beetle *Collops georgianus* which feeds on pollen and seeds of *Diamorpha smallii* (Shure & Ragsdale 1977; King 1987), are largely destructive. Instead, the characteristic plants are typically pollinated by more wide-ranging, flying insects (e.g. Wyatt 1983, 1986). For the most part, the plants appear to have continued to maintain the usual pollination syndromes characteristic of their congeners. The grasses, sedges, and rushes (e.g. *Agrostis eliottiana*, *Cyperus granitophilus* and *Juncus georgianus*) are wind-pollinated. The aquatic *Amphianthus pusillus* is not water-pollinated, but rather insect-pollinated like its relatives in the Gratiolaceae of the Scrophulariaceae. *Tradescantia hirsuticaulis* is pollinated primarily by syrphid flies; *Senecio tomentosus*, by butterflies; and *Sedum pusillum*, by small native bees and flies. Few species are bird-pollinated, but this is true of the flora as a whole, probably reflecting the depauperate nectarivorous avian fauna, a single species, the ruby-throated hummingbird (*Archilocus colubris*). Some plant species associated with woods margins near outcrops (e.g. *Bignonia capreolata* and *Aesculus pavia* × *A. sylvatica* hybrids) are regularly visited by this species (dePamphilis & Wyatt 1989). Even when species with highly unusual pollinator relationships occur on the outcrops, they seem merely to have brought these coevolved mutualisms along with them (e.g. *Yucca filamentosa* and the moth *Tegeticula yuccasella*; Pellmyr *et al.* 1996).

The one exception to this generalisation is *Diamorpha smallii*, which has been reported to be effectively pollinated by ants (Wyatt 1981; Wyatt & Stoneburner 1981). The native ants *Formica schaufussi* and *F. subsericea* regularly visit the flowering plants to feed on the small quantities of nectar produced. In doing so, they pick up large numbers of pollen grains on their unusually hairy bodies, presumably transferring them between individuals of this incompatible species. Tests of pollen applied to ant bodies have shown that viability remains high even after several hours (*unpubl. data*), suggesting that these ants do not secrete substances that kill pollen, as many ant species do (Peakall & Beattie 1987).

With respect to vectors for fruit and seed dispersal, the situation is much the same as for pollinators; the characteristic plants show much the same syndromes as their congeners and as the Piedmont flora as a whole. Most species are moved locally by water during convective storms and by wind during occasional wind storms. If anything, however, the species appear to show



- 2 Photographs illustrating some of the characteristic granite outcrop habitats and plants described in the text. **Plate 1.** Stone Mountain, near Atlanta, Georgia, is a 237-hectare granite dome. Such steeply sloping exposures belie the name "flat rocks," which is commonly applied to granite outcrops in the south-eastern United States. **Plate 2.** A small, flat granite outcrop from eastern Alabama. Vegetation mats develop as soil accumulates in depressions weathered in exposed granite. These microcosms represent different stages of succession: *Diamorpha smallii* (Crassulaceae), a red-bodied succulent, dominates the shallow pool to the left; fruticose lichens and *Andropogon virginicus* (Gramineae) are abundant in the deeper depression to the right. **Plate 3.** Indicative of the hot, dry environment on granite outcrops is the stem succulent *Opuntia humifusa* (Cactaceae). Here it flowers in mid-May on a granite outcrop in Alabama. **Plate 4.** Vegetation mats over granite develop concentric zones, with earlier colonists displaced to shallower soil at the edges. Here, progressing toward the center, we see *Diamorpha smallii* (Crassulaceae), *Arenaria uniflora* (Caryophyllaceae), *Senecio tomentosus* (Compositae), and *Andropogon virginicus* (Gramineae). **Plate 5.** A large rock-rimmed pool on Heggie's Rock, near Augusta, Georgia, holds water between rainstorms during winter (December-March). This is the type locality for the endangered mat-forming quillwort, *Isoetes tegetiformans*. **Plate 6.** Two other endangered species that grow as aquatics in the rock-rimmed pools are *Amphianthus pusillus* (Scrophulariaceae) and *Isoetes melanospora*. *Amphianthus* is a monotypic genus that produces long stalks bearing two floating leaves, between which a single, white flower emerges. **Plate 7.** Characteristic of the many winter annuals that occur on granite outcrops, *Sedum pusillum* (Crassulaceae) germinates in fall and overwinters as a frost-resistant rosette. It grows in moss mats of *Hedwigia ciliata*, typically in the shade of *Juniperus virginiana* (Cupressaceae) trees. **Plate 8.** *Tradescantia hirsuticaulis* (Commelinaceae) occurs in the thin woods fringing rock outcrops. Unlike most of the other endemics that have been studied to date, this species has relatively high levels of genetic variation. **Plate 9.** Another winter annual restricted to granite outcrops, *Arenaria uniflora* (Caryophyllaceae) flowers early in the spring. It has been hypothesised that competition for pollinators between the relatively large-flowered, out-crossing plants shown here and another species (*A. glabra*) with even larger flowers has served as the stimulus for the evolution of self-pollination in geographically marginal populations in Alabama and the Carolinas. **Plate 10.** The flowers of *Talinum mengesii* (Portulacaceae) are open for only a few hours early in the afternoon. In addition to strong spatial separation of the anthers and pistil (herkogamy), out-crossing is promoted by a unique pollen germination delay mechanism.

adaptations against too much dispersal. Long-distance transport, for the most part, would likely deliver a propagule to the inhospitable matrix of forest in which the islands of exposed rock occur. An example of this loss of dispersibility, which characterises many island floras (Carlquist 1974), is *Diamorpha smallii*, which differs from its close relatives in the genus *Sedum* by producing fruits that dehisce by a tear-shaped flap at the back of the follicle (Sherwin & Wilbur 1971). This results in the seeds being dropped directly below the parent plant, where they lie dormant during the hot, dry summer.

I suspect that there may occasionally be directed long-distance dispersal of seeds between outcrops. Birds, such as killdeer, often visit the outcrops to drink from the pools and to forage for invertebrates in the seepage areas at the outcrop margins (*pers. observations*). In doing so, they may inadvertently pick up plant propagules in the mud on their feet. After travelling to another outcrop, the propagules may be washed off. It is possible that hawks and vultures, which are also commonly seen in the vicinity of the outcrops drinking from pools, hunting, and riding thermals, act similarly as dispersal vectors. In any event, however, gene flow via these dispersal vectors is likely to be rare. Other species, like the Georgia oak (*Quercus georgiana*), pose additional difficulties, as their seeds are very large. Rarely, they may be transported between outcrops by blue jays, which are known to collect and cache seeds of oaks (Darley-Hill & Johnston 1981).

With the exception of *Isoetes*, plants whose primary mode of dispersal is spores do indeed seem to be moved long distances by the wind. For example, *Pellaea wrightiana* is a common fern of rocky cliffs in the southwestern United States. Some years ago it was collected from a single granite outcrop in North Carolina, more than 1 600 km from the nearest populations in central Texas (Wagner 1965). Similarly, *Astrolepis sinuata*, a fern otherwise restricted to west Texas and northern Mexico, has been collected recently from a small granite outcrop in western Georgia (J R Allison, *pers. comm.*). The fern *Pilularia americana* and a number of lichens and mosses also show long-range disjunctions to outcrops in the southeast (Wyatt & Stoneburner 1982). The species of *Isoetes* that are endemic to granite outcrops in the southeastern United States are a notable exception to the pattern shown by homosporous pteridophytes. Genetic markers suggest that gene flow between outcrop populations of *I. piedmontana*, *I. melanospora*, and *I. tegetiformans* is very low (Van De Genachte & Wyatt, unpublished). This may be due to the fact that successful colonisation by these heterosporous plants requires simultaneous dispersal not only of the small microspores, but also of the much larger (and presumably, less dispersible) megaspores.

Many of the characteristic granite outcrop species in the southwestern United States are characterised by high rates of outcrossing. Unlike the situation in many island floras (e.g. Hawaii; Carlquist 1974), however, there is not a disproportionately high number of dioecious species. The Piedmont flora as a whole is rather depauperate in dioecious species, which constitute only about 3.4% of the flora (Conn *et al.* 1980). The dioecious species that are common on outcrops are mostly woody taxa with wider ranges off the outcrops (e.g. *Juniperus virginiana*, *Smilax smallii*, *Forestiera ligustrina*). Dioecy is rare among annuals (Conn *et al.* 1980); thus, it is interesting to note that *Rumex hastatulus* is

among the weedy species that may once have been restricted to granite outcrops (see below).

Among the known outcrossers on granite outcrops are taxa demonstrated to be genetically self-incompatible (e.g. *Diamorpha smallii*, Wyatt 1981; *Tradescantia hirsuticaulis*, unpubl. data) and those with well-developed herkogamy (e.g. *Talinum mengesii*, Murdy *et al.* 1970) or dichogamy (e.g. central populations of *Arenaria uniflora*, Wyatt 1984). Murdy & Carter (1987) discovered a unique pollen germination delay mechanism in *Talinum mengesii*. They reported that pollen grains deposited on the stigma during the few hours that each flower was open in the early afternoon failed to germinate immediately, but rather were delayed for up to 90 minutes. They speculated that this had the effect of opening up the range of mates siring seeds on each plant and of intensifying gametophytic competition.

Even more numerous, however, are the many taxa, including some in the same genera listed above, that have evolved self-fertilisation. Self-compatibility has been documented in *Sedum pusillum* (Wyatt 1983), which also showed evidence of outbreeding depression, and *Zephyranthes atamasco* (Broyles & Wyatt 1991). *Talinum teretifolium* is self-compatible and highly self-pollinating relative to its diploid progenitor, *T. mengesii* (Murdy 1968; Murdy *et al.* 1970; Murdy & Carter 1985). In this it contrasts sharply with the diploid/allotetraploid species-pair *Sedum pusillum*/*Diamorpha smallii*, in which the former is self-compatible and the latter, self-incompatible. The marginal populations of *Arenaria uniflora* studied by Wyatt (1984) are self-compatible and strongly self-pollinating. This also appears to be true for *Phacelia dubia* var. *georgiana* (Levy 1988). I am inclined to discount early reports of a "balanced breeding system" in *Amphianthus pusillus*, in which plants produce immersed cleistogamous flowers at the base of the rosette and emerged chasmogamous flowers in the axils of paired bracts at the tips of elongated, floating branches (e.g. Pennell 1935). The "cleistogamous" flowers appear to be merely an earlier developmental stage, observed prior to elongation of the floating branch. True "hydroautogamy" appears to be rare (Philbrick 1991).

Surprisingly few of the species endemic to granite outcrops have been analysed for genetic population structure. Using horizontal starch-gel electrophoresis, Wyatt *et al.* (1992) found low genetic variation in outcrop populations of *Arenaria uniflora*; the percentage of loci polymorphic per population averaged 17.9%; mean number of alleles per locus, 1.0; and expected heterozygosity, 0.048. The selfing populations at the margins of the range were often fixed for alleles that were polymorphic in the central, outcrossing populations. This led to a remarkably high value for G_{ST} , which expresses the proportion of the total gene diversity that exists as differences among populations. The G_{ST} of 0.572 indicates very strong genetic differentiation between outcrops. Similar results were obtained for *Isoetes melanospora* (25.4%, 1.32, and 0.069) and *I. tegetiformans* (12.5%, 1.14, and 0.020) by Van De Genachte & Wyatt (unpublished). Again, strong genetic differentiation was seen for these species ($G_{ST} = 0.513$ and 0.217, respectively). In contrast, Godt & Hamrick (1993) found high levels of genetic variation in

Tradescantia hirsuticaulis (53.5%, 1.72, 0.157). Nevertheless, the isolated populations were more strongly differentiated than expected ($G_{ST} = 0.183$). Only in *T. hirsuticaulis* have gene flow estimates > 1 been estimated ($Nm = 2.150$; Godt & Hamrick 1993). Presumably, there is very little gene flow between outcrop populations of *Arenaria* and *Isoetes*, and genetic drift therefore can have strong effects on these isolated populations.

Recently, Levy *et al.* (1996) have analysed genetic variation in *Phacelia* using restriction fragment length polymorphisms in chloroplast-DNA. They found surprisingly high levels of intraspecific polymorphism, especially in populations of the granite outcrop endemic *Phacelia dubia* var *georgiana*. Levy *et al.* (1996) discounted the likelihood of these polymorphisms being due to gene flow between outcrop populations.

At least two of the most characteristic species endemic to granite outcrops have originated via allopolyploidy. Using isozymes as genetic markers, Murdy & Carter (1985) showed that *Talinum teretifolium* is an allotetraploid that combines genomes from diploid *T. mengesii* and diploid *T. parviflorum* from the west-central United States and one locality in Alabama (formerly called *T. appalachianum*; Carter & Murdy 1985). Despite conflicting evidence for some loci and a disquietingly high number of "null" alleles, they were able to reject clearly the alternative hypothesis that *T. calycinum* was the second progenitor. Although definitive proof remains elusive, it seems clear that *Diamorpha smallii* also is an allotetraploid ($n = 9$), one of whose progenitors is diploid *Sedum pusillum* ($n = 4$). As Baldwin (1940) suggested, the other progenitor perhaps should be sought among those annual species of *Sedum*, such as *S. nuttallianum* of the west-central United States, with $n = 5$. Alternatively, *D. smallii* could be related to *Parvisedum*, a small genus of California and northern Mexico with $n = 9$ (Clausen 1975). Murdy (1968) also suggested that the outcrop endemic *Cyperus granitophilus* may have originated via autopolyploidy from the more widespread *C. aristatus*.

For allopolyploid speciation, hybridisation is a necessary prerequisite. Interestingly, the outcrops seem to represent "hot spots" for hybridisation. To some extent, this may be due to their offering a wide range of habitats, some of which mimic those of other physiographic provinces. For example, the Coastal Plain *Senecio tomentosus* extends its range into the Piedmont on the outcrops, where it comes into contact with *S. anonymus*. Chapman & Jones (1971) documented hybridisation between these species, showing that the F_1 hybrids have reduced pollen fertility. Other species notable for their tendency to hybridise in proximity to granite outcrops include *Quercus* (*Q. georgiana* $\times$ *Q. nigra*, unpubl. data), *Aesculus* (*A. pavia* $\times$ *A. sylvatica*, de Pamphilis & Wyatt 1989, 1990), and *Isoetes* (*I. tegetiformans* $\times$ *I. piedmontana*, Van De Genachte & Wyatt unpublished; *I. melanospora* $\times$ *I. piedmontana*, Allison 1993).

It would also appear likely that the geographical isolation of populations on granite outcrops could lead to allopatric speciation, especially following a long-distance dispersal event. This process may underlie the origin of the endemics *Phacelia dubia* var *georgiana* and *P. maculata*

(Murdy 1966, 1968; Levy 1991a). Levy's (1991b, 1996) subsequent experimental studies have suggested how reproductive barriers can arise as taxa diverge and strongly hint that new incipient varieties are still being formed. Two other outcrop species that Murdy (1968) advanced as examples of ecogeographical differentiation are *Portulaca smallii* and *Rhynchospora saxicola*. This interpretation, however, may be backwards (see below), as the Coastal Plain habitats occupied by their presumed progenitors are probably younger than the Piedmont outcrops.

Much interest has focused on two of the outcrop endemics that appear to be highly isolated in their families and to have no close relatives; *Amphianthus pusillus* and *Viguiera porteri*. McVaugh (1943) used the former to argue for the great antiquity of the outcrop flora and the latter to show an affinity with the Madro-Tertiary flora of the southwestern deserts, as all other species of *Viguiera* are restricted to that region. More recent evidence from phylogenetic reconstructions based on chloroplast-DNA gene sequences shows that *Amphianthus* is closely allied with the Gratiolaceae, including *Gratiola*, *Bacopa* and *Mecardonia*, among others (dePamphilis, unpubl. data). Similarly, Schilling & Jansen's (1989) data concur with Schilling & Heiser's (1981) suggestion that *V. porteri* is not a *Viguiera* at all, but rather a *Helianthus*.

The weedy species commonly observed on granite outcrops are a very limited subset of the total Piedmont weed flora. The group includes few, if any, exotics (McVaugh 1943). This observation led Wyatt & Fowler (1977) to propose that these species may, indeed, have once been endemics restricted to outcrop habitats. They possessed a number of features, however, that enabled them to invade disturbed habitats, such as old fields, following the arrival of humans. Marks (1983) has advanced this same argument. Thus, for example, rather than understanding the ecotypic adaptation of the old-field dominant grass *Andropogon virginicus* to outcrops, as Chapman & Jones (1975) did, it might be more appropriate to read the evolutionary process in the opposite direction.

Broadening this view a bit, it might be useful to consider the outcrops as the possible original evolutionary springboard for such present-day widespread Coastal Plain plants as *Rumex hastatulus*, *Linaria canadensis*, and *Crotonopsis elliptica*. These pre-eminent weedy plants of the Coastal Plain may have perfected their ability to grow in open, disturbed areas of poor, sandy soil while existing primarily on granite outcrops. When similar habitats became available on the Atlantic and Gulf Coastal Plains, they may have undergone range expansion. Other species that appear to fit this pattern include *Nothoscordum bivalve*, *Schoenolirion croceum*, *Trifolium carolinianum*, *Forestiera ligustrina*, and *Houstonia pusilla*.

Acknowledgments: I thank the organisers of this symposium, S D Hopper, D Edward, and P Withers, for the invitation to participate and the opportunity to write on this subject. I also thank S D Hopper for stimulating my thinking about the unique habitats and organisms of granite outcrops. He and a long list of students and colleagues have kept my interest alive for many years; among others, these include J Allison, M L Burbank, S B Broyles, M E B Carter, C W de Pamphilis, B Ellwood, E A Evans, J W Glasser, M J W Godt, J L Hamrick, P S King, F Levy, W H Murdy, D J Shure, J L Sorenson, A Stoneburner, and E E Van De Genachte.

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The geobiological interface: Granitic outcrops as a selective force in mammalian evolution

M A Mares

Oklahoma Museum of Natural History and Department of Zoology, University of Oklahoma,
Norman, Oklahoma 73019 USA email: mmares@ou.edu

Abstract

Granite outcrops appear with regularity in various parts of the world. They may be associated with mountains, or they may appear in areas that today have little other topographic relief than the outcrops themselves. Wherever granitic agglomerations are found, however, their influence on the biota of a region is profound. Rocks influence both microhabitat and macrohabitat for plants and animals. In some cases, the rocky habitats permit a more mesic microhabitat to develop within a generally more xeric region. Such microclimatic influences may permit the establishment of trees and the maintenance of green leaves, even during droughts. For mammals, in addition to the increased availability and predictability of food, the rock habitat itself provides shelter, amelioration of climatic variables and, in some cases, a resource that is defensible by the mammals. However, the rock habitat is one that also demands special adaptations by mammals that specialize toward a rupicolous existence. Such specializations include morphological, ecological, and behavioral traits that develop in direct response to the selective forces required to inhabit rocks. These influences may extend even to mating systems, where the unusual habit of harem polygyny develops among small mammals whose males manage to defend the rock resource against other males, thereby accruing females. Because of their influence on macro- and microhabitat, granite outcrops also have a regional influence on biodiversity, increasing significantly the number of species that occur in areas that are frequently rather depauperate due to their semiarid or arid nature. The responses of mammal faunas in Africa and South America to granite outcrops is used to compare and assess the importance of these rock outcrops on aspects of mammalian biology.

Introduction

The diversity of mammals in any particular region has been related to many factors, including climate, age of the fauna, past formation of refugia, productivity, environmental predictability, competitors and predators, size of the area, and other factors (see Rosenzweig 1995 for review). In general, the effect of physical structure of the environment (as opposed to the biotic structure) on patterns of diversity and richness has been given less attention, although there has been some work on the effects of dunes on small mammal species richness (Brown 1973). Even in this study, however, the dunes have been considered mainly as habitats that supported fewer species of mammals than the surrounding better-vegetated areas. In a more detailed analysis of regional patterns of species diversity, Brown (1975), found that in a xeric North American desert system, overall species diversity of rodents is strongly influenced not only by α -diversity (species occurring in a single locality), but by β -diversity (species turnover) as well, since many species have restricted distributions in deserts. Of course, at a macroscale, the influence of mountain ranges and other major topographic features has long been known to have a major influence on species richness through increased habitat diversity, altitudinal effects, refugial formation, and other factors (e.g. Simpson 1964; Wilson 1974; Brown 1978; Mares & Ojeda 1982; Mares 1992; Willig & Sandlin

1991). At a smaller scale, the influence of structural features of the environment on patterns of mammalian diversity and richness are less apparent.

One regularly occurring structural feature of habitats scattered throughout the world is granite outcrops. As has been shown in other papers in this issue, the influence of these outcrops on plants, microorganisms, animals, and people are extensive. There has not been a great deal of research on the influence of granite outcrops on mammals, although there are some notable exceptions, particularly in examining the influence of rocks on the biology of small mammals in southern Africa and South America. Hoeck (1975, 1982) and Hoeck *et al.* (1982), for example, studied hyraxes in the Serengeti and found that the rocks themselves were a critical resource. The males of these rock specialists defended the rock-piles in such a way that they were able to attract and keep multiple females as mates. The females also required access to the rocks for food, water, protection, and nesting space. Thus the male hyraxes, by virtue of being able to control access to the rocks, formed harems; harem polygyny is an unusual behavioral trait in a small mammal. Lacher (1981) studied a caviid rodent *Kerodon rupestris* (guinea pig family) in eastern Brazil, that was also highly specialized for living on granitic outcrops within a larger dry tropical scrubland, the Caatinga. He found that *Kerodon*, which strongly resembled a hyrax externally, also defended rock-piles and, like the hyraxes of Africa, also accrued females to form harems.

In a multivariate comparison of morphological, ecological, and behavioral characteristics of rock-dwelling

small mammals from throughout the world, Mares & Lacher (1987) showed that mammals inhabiting rocks have developed a host of similar adaptations, including specific morphological, ecological, and behavioral traits, such as specialized foot structure, general body form, dietary similarities, similar activity periods, alarm calls, communal defaecation, and a propensity to form harems. The formation of harems seems to result from the ability of the males to defend portions of the rock-piles, thus controlling a resource that is required by the females and their offspring. In order for a female to have access to the critical rock resource, and all of the ecological factors associated with the rocks, she must enter into the harem of the male. Mares & Lacher interpreted this to be an example of resource defense polygyny (Emlen & Oring 1977), a pattern that has also been documented for such non-rock specialists as tree-dwelling bats (the Neotropical emballonurid, *Saccopteryx bilineata*) that control access to cavities in the trees by defending them against other males, thus developing harems of females that require access to the hollow tree in order to raise their young (Bradbury & Emmons 1974). Mares & Lacher (1987) also made clear that becoming a rock specialist requires a broad array of adaptations. Moreover, these adaptations are similar from one part of the world to another, regardless of the phylogenetic history of the organisms in question (they examined 24 species of mammals in 17 genera, 12 families and 4 orders).

At a larger scale, rocks have also been shown to have an influence on the regional species richness of small mammals, especially in southern Africa, where this phenomenon has been examined in some detail. Coetzee (1969), for example, noted that "The distribution of animal life (especially the small mammals) is largely

influenced by rocky outcrops"; he provided a list of 28 species of mammals that frequent rocky outcrops in Namibia. He later (Coetzee 1983) supported these observations with an analysis of mammalian geographic ranges. In a more detailed ecological study in Namibia, Withers (1979) examined the small mammals of an inselberg (isolated rocky outcrop) community and found that both rock specialists and more-generalist species comprise the community. The community ecology of the mammals was greatly affected by microclimate effects of the inselberg and its associated vegetation, as opposed to the surrounding sparse desert habitat. Although he did not conduct a regional analysis of distributional patterns, Withers showed clearly that the rock-piles were a major factor in small mammal species richness in the Namib Desert. Among the areas used by Mares & Lacher (1987) in their broadly comparative study of rock-dwelling mammals were the Namib Desert, the Caatinga, and the Andean region of Argentina. Mares *et al.* (1981) and Mares *et al.* (1985a) had shown that rock-piles in the Caatinga had a significant influence on both species richness and persistence, and Mares (1993) provided information showing that rocky habitats were important components of generic richness for small mammals in Andean deserts.

Here, I extend the comparisons of the Namib Desert, Brazilian Caatinga, and Argentine Andes to consider the effect of granite outcrops on the structure of the entire mammalian community in these three areas. I first provide a brief comparative review of the regions and their history to permit a greater understanding of how mammals have adapted to rock-piles, a significant abiotic structural component of their habitat in three markedly different drylands on two southern continents.



Figure 1. The interface of sand, river, and rock in the Namibian Desert near Gobabeb. The light-colored material in the foreground is sand at the edge of the riverine vegetation of the Kuiseb River. On the other side of the river are granitic outcrops. Barely visible in the background beyond the rocks is the gravel plain of the Namib. Both the rocky areas and the river support vegetation that is quite different from either of the two major habitats (the dune fields and the plains). The mammals of the rocks are also distinct from those of the other major habitats.



Figure 2. A broad granite surface exposure (lajeiro) in the Caatinga of northeastern Brazil. In the background are rocky outcrops (serras). Lajeiros collect water and form micro-communities of plants (evidenced by the cacti, shrubs and grasses in the center of the photo). Serras support shrub and tree communities that are distinct in physiognomy and persistence of green vegetation from the surrounding Caatinga scrub forest. The mammals of the lajeiros, serras, serrotes (larger outcrops that form small hills), and chapadas (outcrops that are larger still, forming small mountains) are very distinct from those of the non-rocky areas.

Methods

Study Areas

Namibia. The Namib Desert, a coastal desert, is one of the oldest deserts on earth (Seely 1987; Ward & Corbett 1990). It is also among the world's driest deserts, with much of the precipitation being received as fog (Walter 1986). Over much of the area there is only sparse vegetation, whether on the gravel plains or on the enormous dune "sea" that characterize the region. There are, however, areas that support much more vegetation than the habitats that surround them, and these include rivers (e.g. Kuiseb) and granite outcrops (inselbergs and other outcrops), where trees, shrubs, and grass may be present (e.g. Theron *et al.* 1980; Seely 1987). In some places, such as near the Desert Research Station at Gobabeb, the various habitats abut one another. Here fields of moving dunes pour over granitic outcrops that line the Kuiseb River valley, north of which an abrupt transition to gravel plains occurs (Fig 1). The history of the Namib region, as well as the general ecology of the desert and its flora, fauna, and habitats has been fairly well studied in recent years (e.g. Coetzee 1969, 1983; Stuart 1975; Joubert & Mostert 1975; Werger 1978; Henschel *et al.* 1979; Withers 1979; Tilson 1980; Tilson *et al.* 1980; Walter 1986; Seely 1987, 1990). Although seldom examined specifically, researchers have found that inselbergs play a major role in the maintenance of mammal species richness in this desert by virtue of the microhabitat provided by the rocks, which includes floristic and climatological influences.

Caatinga. The Caatinga of northeastern Brazil has also received a great deal of attention from biologists in recent years (e.g. Markham 1972; Eiten 1974; Webb 1974; Reis 1976; Ab'Sáber 1977; Lacher, 1981; Willig, 1983; Mares *et*

al. 1981, 1985a; Andrade-Lima 1982). This region of more than 650 000 km² lies well within the tropics and undergoes periodic pronounced droughts at irregular intervals during which most of the vegetation loses its leaves. Its vegetation is much like a thorn scrub in aspect. Populations of small mammals die back during the droughts, and there is great misery among the human inhabitants of the regions as livestock die and water for human use becomes scarce. During wet years, which are more common than dry years, the area is a lush, low, green forest and mammals and other wildlife species are abundant. During droughts, the Caatinga resembles the semiarid chacoan thorn scrub of western Argentina, including the presence of many types of tree cacti (*Cereus*) and other cacti that frequent the areas of open granite (termed "lajeiros" in Portuguese). The Caatinga also has granite outcrops varying in size from isolated boulder piles to small hills (Fig 2). It is in these outcrops that the area's only endemic mammal is found, the caviid rodent, *Kerodon rupestris*, a rupicolous species specialized for life on the isolated rock-piles. Mares *et al.* (1985a) hypothesized that these rock-piles play a major role in maintaining mammal diversity in the Caatinga by offering a microhabitat refuge to mammals during the periodic droughts. They suggested that after severe droughts, the Caatinga, especially the core of the region, is in large part re-colonized by small mammal populations that managed to persist in the more mesic microclimate associated with the rock-piles.

Argentine Andes. The Andes of westcentral Argentina also support vast areas of granite outcrops, interspersed with other types of rock (Videla & Suarez 1991), and with flat plains located between mountain massifs (Fig 3). The rocky areas of the Andes are also home to a number of rock specialists among small mammals (Mares



Figure 3. Rock outcrops in an inter-Andean valley near the town of Uspallata, Mendoza Province, Argentina at an elevation of about 2,000 m elevation. The scrub desert of the gravel plains, which mainly supports creosote bush (*Larrea*), gives way to different communities of plants on the rock outcrops. The area supports a number of mammals that are specialized for life in the rocks.

& Lacher 1987; Ojeda & Mares 1989; Mares 1993; Braun & Mares 1996). Much of the high Andes of Argentina includes arid habitats that support either sparse grasses or scattered shrubs (Mares *et al.* 1985b). Although the mammals of this region have not been as well studied as those of the previous two areas, the rocky areas appear to function as important microhabitats for species persistence through their effect on microclimate, plant distribution, and as places for shelter (*e.g.* Pearson 1948; Pearson & Ralph 1978).

Data

Published data on mammals and their habitats were examined for the three areas described above. In particular, information was sought that specifically referenced the use of rocks by the mammals in these regions. Species lists were examined for the areas in question, and information was obtained on surveys of the mammals of the areas that included information on the entire mammal fauna, rather than being limited to small mammals. References utilized are included throughout this report. Additionally, my students and I conducted extensive research on mammals of the Caatinga in the 1970s and on mammals in the Andean and pre-Andean mountains during the last three decades (*e.g.* Mares *et al.* 1989, 1997; Barquez *et al.* 1991). Additionally, I was able to spend a brief field period in Namibia in 1995.

Effects of Rock-piles

Few studies have considered the ecological effects of rock-piles on mammals. While not designed to measure the ecological effect of rocks on mammals *per se*, Withers (1979) found that the microclimate of the rocky inselbergs he examined supported different plant species from the surrounding desert, and this microhabitat-plant

association was related to the abundance of small mammals, as well as to small mammal species richness. Lacher (1981) and Streilein (1982a,b,c) also found that the rocky habitats provided refugia for small mammals during periods of drought, when the green vegetation and occasional pools of water offered escape from the harsh aridity of the surrounding habitat. Water availability has been shown to be an important factor in reproduction of small mammals in both Namibia and the Caatinga (Christian 1976, 1980; Withers 1979; Streilein 1982c,d), although no research has shown how water might effect small mammals in the Andes. Below, I discuss various effects of rocky habitats that are related to mammal occurrence. A taxonomic listing of mammals in these three areas, as well as indications as to whether or not the taxa are rock specialists, is given in Table 1, whereas a list of rock specialists in the three areas is given in Table 2.

Microhabitat effects of rocks

As noted, many studies have shown that rocky areas provide a microhabitat that differs significantly from the surrounding region. Clearly, the microhabitat effects of rocks on climate, plants, and animals are interrelated in complex ways, but it is instructive to tease apart the various factors that interact to influence mammals in order to understand more clearly the role that rocks play in patterns of mammalian richness and persistence. In the three arid to occasionally semi-arid habitats considered in this report, the rocky substrate contributes in the following ways to mammalian persistence and richness.

Structure. Rocks form a major structural component of the ecosystem, especially in areas that would have little topographic relief were it not for the rocks themselves. The structural effect of rocks can be considered to be a first-level effect of the rocks on the community of

Table 1

Orders, families, and genera of mammals inhabiting granitic outcrops in Namibia (in the general environs of Gobabeb); in the Brazilian Caatinga (near Exu, Pernambuco); and in the Andes of central Argentina (Mendoza Province). Rock specialists (species that are highly adapted to inhabit rocks and that are generally limited to rocky outcrops) are denoted by an asterisk (*). O = order; F = family. Common names are in parentheses. Based on information for Africa in Coetzee (1969), Stuart (1975), Withers (1979), Skinner & Smithers (1990); for Brazil in Mares *et al.* (1981, 1985), Streilein (1982a,b,c); for Argentina in Barquez *et al.* (1991), Mares (1993), Mares *et al.* (1985b, 1997), and Mares (unpublished data).

Namibia	Caatinga	Argentine Andes
O. Macrosceloidea	O. Didelphimorphia	O. Didelphimorphia
F. Macroscelididae	F. Didelphidae	F. Didelphidae
(elephant shrews)	<i>Monodelphis domestica</i> (Gray short-tailed	<i>Thylamys pusilla</i> (Mouse opossum)
<i>Elephantulus rupestris</i> *	opossum)	
<i>Elephantulus intufi</i>	<i>Didelphis albiventris</i> (White-eared	O. Rodentia
<i>Macroscelides proboscideus</i>	opossum)	F. Abrocomidae
O. Chiroptera	O. Chiroptera	<i>Abrocoma vaccarum</i> * (Chinchilla rat)
F. Vespertilionidae	F. Molossidae	F. Chinchillidae
<i>Eptesicus hottentotus</i> (Long-tailed house	<i>Molossops mattogrossensis</i> * (Flat-headed	<i>Chinchilla brevicaudata</i> * (Chinchilla)
bat)	free-tailed bat)	<i>Lagidium viscascia</i> * (Mountain vizcacha)
F. Molossidae	O. Rodentia	F. Muridae
<i>Sauromys petrophilus</i> * (Flat-headed free-	F. Caviidae	<i>Akodon andinus</i>
tailed bat)	<i>Kerodon rupestris</i> * (Rock cavy)	<i>Eligmodontia typus</i>
O. Primates	<i>Galca spixii</i> (Cavy)	<i>Graomys griseoflavus</i>
F. Cercopithecidae	F. Dasyproctidae	<i>Phyllotis darwini</i> *
<i>Papio ursinus</i> (Chacma baboon)	<i>Dasyprocta prymnolopha</i> (Agouti)	O. Carnivora
<i>Cercopithecus aethiops</i> (Vervet monkey)	F. Echimyidae	F. Canidae
O. Hyracoidea	<i>Thrichomys apereoides</i> * (Punaré)	<i>Pseudalopex culpaeus</i> (Andean red fox)
F. Procaviidae	O. Carnivora	F. Mustelidae
<i>Procapra capensis</i> * (Rock dassie)	F. Canidae	<i>Galictis vittata</i> (Grisson)
O. Rodentia	<i>Cerdocyon thous</i> (Forest fox)	F. Felidae
F. Petromuridae	F. Mustelidae	<i>Lynchailurus pajeros</i> (Pampas cat)
<i>Petromus typicus</i> (Dassie rat)	<i>Galictis vittata</i> (Grisson)	<i>Felis concolor</i> (Puma)
F. Muridae	<i>Conepatus semistriatus</i> (Hog-nosed	
<i>Aethomys namaquensis</i> * (Namaqua rock	skunk)	
mouse)	F. Felidae	
<i>Petromyscus collinus</i> * (Pygmy rock mouse)	<i>Felis concolor</i> (Puma)	
F. Hystricidae	<i>Felis yagouaroundi</i> (Jaguarundi)	
<i>Hystrix africaeaustralis</i> (Porcupine)	<i>Felis onca</i> (Jaguar)	
O. Lagomorpha		
F. Leporidae		
<i>Pronolagus rupestris</i> * (Smith's red rock		
rabbit)		
O. Artiodactyla		
F. Bovidae		
<i>Oreotragus oreotragus</i> * (Klipspringer)		
<i>Oryx gazella</i> (Gemsbok)		
O. Carnivora		
F. Canidae		
<i>Vulpes chama</i> (Cape fox)		
<i>Canis mesomelas</i> (Black-backed jackal)		
F. Mustelidae		
<i>Ictonyx striatus</i> (Striped polecat)		
<i>Helogale parvula</i> (Dwarf mongoose)		
F. Hyaenidae		
<i>Crocuta crocuta</i> (Spotted hyaena)		
<i>Hyaena brunnea</i> (Brown hyaena)		
F. Felidae		
<i>Felis libyca</i> (African wild cat)		
<i>Felis nigripes</i> (Small spotted cat)		
<i>Panthera pardus</i> (Leopard)		

mammals (*i.e.* an effect on the abiotic components of the habitat). The rocks contribute to environmental complexity in a number of ways. They offer sites for shelter, where both small and large mammals may place their nests or dens to raise their young in a stable microclimate that is relatively secure from predators and competitors. For example, in a remarkable example of

convergent evolution, the granite outcrops of Namibia support a small rock-specialized molossid bat, *Sauromys petrophilus*, that has an extremely flat body and is adapted to live in the cracks of exfoliating granite (Skinner & Smithers 1990). In the Caatinga, there is also a flattened molossid bat, *Molossops mattogrossensis*, that is specialized for living in exfoliating granite (Willig &

Table 2

Genera of rock-specialist mammals inhabiting granitic outcrops in Namibia (in the general environs of Gobabeb); in the Brazilian Caatinga (near Exu, Pernambuco); and in the Andes of central Argentina (Mendoza Province). These species, representing among the three areas 6 orders and 11 families, and including 4 endemic families and 9 endemic genera (endemic to the rocky areas in the region) would not be in the arid area in question if the rock resource were not present.

Namibia	Caatinga	Andes
<i>Elephantulus</i> *	<i>Molossops</i> *	<i>Abrocoma</i> *
<i>Sauromys</i> *	<i>Kerodon</i> *	<i>Lagidium</i> *
<i>Pronolagus</i> *	<i>Thrichomys</i> *	<i>Chinchilla</i> *
<i>Procavia</i> *		
<i>Petromus</i> *		
<i>Petromyscus</i> *		
<i>Oreotragus</i> *		

Jones 1985). By virtue of their elevation above the surrounding habitat, rock outcrops also offer sites for observation posts, where predators can be detected, or territorial communication can occur. For example, the hyraxes of Namibia, the caviids of the Brazilian Caatinga, and the chinchillid rodent (*Lagidium*) of the Argentine Andes (Pearson 1948) are all diurnal herbivores that use the rocks for observation points to detect predatory attacks from the air or from the ground. All use sentinels that give warning calls as predators are sighted (Mares & Lacher 1987). Similar behavior in using the structure of the rocky habitat has been shown for the petromurid rodent, *Petromus*, in Namibia, and many other species as well (Mares & Lacher 1987). Even large mammals, such as the spotted hyaena (Family Hyaenidae, *Crocuta crocuta*) and the klipspringer (Family Bovidae, *Oreotragus oreotragus*) use the rocks for dens (hyaena) or for lookout posts (antelope). Additionally, the rocks offer sites for chemical communication, where communal defaecation piles, a common trait of rock-dwelling mammals (Mares & Lacher 1987), may function in territorial and other communication by elevating the piles of faeces high in the air where the scent can be carried for long distances; see, for example, Branch (1993) for information on how the plains vizcacha (Chinchillidae, *Lagostomus maximus*), a relative of the mountain vizcacha, *Lagidium*, uses communal sites for phomonal communication. The rocky substrate also functions as sites for capturing water. Granitic outcrops may capture and hold rainfall for extended periods, and this water is important to mammals in arid regions. Additionally, the rocks may act to permit condensation of fog in some areas (e.g. Namibia), thus increasing water availability to mammals (Withers 1979). Rocks also provide sites that are defensible by males, or by groups of related individuals. Mares & Lacher (1987) showed that rock-piles, and the shelter and other resources they offer, are defensible by males of several species, thus permitting them to accrue harems of females by apportioning the rock resource differentially on the basis of sex. How extensive harem formation may be in rock mammals is not yet clear, but it is clearly not uncommon among species inhabiting rocky areas, although it does not appear to be a common reproductive pattern among small mammals that do not defend rocks.

Microclimate. Rocky areas that occur within a more-xeric region offer mesic refugia through microclimate effects. These can also be considered first-level effects of the rocks on the mammal community. Water accumulated by rocks would contribute to micro-changes in humidity. The shelter offered by the rocks, especially in areas where run-off water or fog condensation may accumulate (Withers 1983), will also tend to increase humidity, and thus reduce water loss for mammals that utilize the shelters during arid periods. Similarly, the rocks offer shade during the heat of the day, and a cool refuge during summer or during the dry season. Alternatively, the rocks store heat, thus modifying the microclimate of shelters during cold periods by keeping temperatures elevated above that of the cold desert air. The rocks provide elevated areas where temperature increases rapidly in the morning sun, thus providing points of rapid warming, where mammals can increase their body temperatures quickly before beginning the day's activities. Most rock mammals have been observed to bask in the early morning (Mares & Lacher 1987). Rocks, particularly those that offer deep shelters, provide temperature stability from the outside air which, in arid areas, can undergo pronounced fluctuations. For example, Mares (1975) reported air temperature changes of up to 38 °C over a 24-hr period in the Andes of northwestern Argentina. Rock-piles also provide a diel factor to microclimate, permitting animals to choose from a selection of microclimates throughout the day and night. Because of the structure of rock-piles, animals can utilize different portions of the rocks at different times of day to increase the climatic variability (or stability) of their habitat. For example, sunny portions of the rocks can be used for warming up for some animals, while at the same time others are cooling down in shaded portions. During very wet weather, dry portions of the rock habitat can be sought by mammals when other microsites are too wet for the species in question.

Effects of rock-piles on vegetation. Perhaps one of the most evident second-level effects of rock-piles on mammal communities in an arid region is the effect of the rocks on vegetation. In an area such as the Caatinga, for example, rock-piles support small forests of trees that largely remain green throughout the extended droughts. During wet periods, these refugial forests may be less noticeable, imbedded as they are within the brilliant green scrub forest of the Caatinga, but during droughts, almost the only green vegetation remaining over vast areas is that associated with the rock-piles (Mares *et al.* 1985a). Similarly, in Namibia, the rocks have been shown to support more complex vegetation than much of the surrounding desert (Seely 1987, 1990; Withers 1979). The vegetation of the rocks is often greener for longer periods due to increased water availability afforded by the rocks. Additionally, the granitic outcrops support perennial trees in zones where most of the other vegetation may be low scattered shrubs or short-lived ephemeral plants. The vegetation permits the browsing habit to develop among small mammals (and larger mammals, as well). Thus such disparate species as hyraxes (Order Hyracoidea), rabbits (Order Lagomorpha), and rodents (Order Rodentia) all have evolved rock specialists that browse on the trees and shrubs associated with the rock-piles. Of course, the vegetation contributes enormously

to both habitat complexity, habitat stability, and microclimate. In the Caatinga, the rock-piles are assumed to offer refugia for rock specialists and a wide variety of species that are not rock specialists during periods of drought (Mares *et al.* 1985a). Plants associated with rocks thus offer food, shelter, and other major components of mammal niches throughout the year.

Effect of rocks on mammal species richness

As noted, the rocks have significant effects, both first- and second-level, on mammal communities and on major components of mammal niches, including food, shelter, and microclimate. The rocks, their plants, and their special microclimate, make it possible for many species either to specialize on the rocks and their associated resources (Mares & Lacher 1987), or to live in the rocks when the surrounding habitat is marginal due to drought or other factors (e.g. Withers 1979; Streilein 1982a; Mares *et al.* 1985a). The rocks and their vegetation make possible, for example, a richer invertebrate community, including many insects and arthropods, thus making this group of organisms available to mammalian predators. Thus the existence of certain communities of mammals are only possible because of the rock component of the habitat (Table 2), a fact that can be considered a third-level effect of the rocks on species richness. This community may consist of diurnal browsing rock specialists, such as hyraxes and petromurids in Namibia, caviids and echimyids (*Thrichomys*) in the Caatinga, or chinchillids and abrocomids (*Abrocoma*) in Argentina. However, the rock habitat influences much more than just rock specialists. In Namibia, among small mammals, the rocks harbor *Aethomys*, an insectivorous murid rodent, and *Elephantulus* (Order Macrosceloidea), an insectivorous elephant shrew (Withers 1979). In the Caatinga, the rocks support an invertebrate-feeding marsupial, *Monodelphis domestica* (Streilein 1982a), and in the Andean mountains at lower elevations (up to 2 000 m) insectivorous mouse opossums (genus *Marmosa*) also inhabit the rocks (Mares *et al.* 1989). Thus the rocks add to the complexity of the small mammal community, as well as to the vegetative, structural, and climatological complexity of the habitat itself. Larger mammals, such as the klipspringer (noted above, in Namibia; Tilson 1980), the huemul deer (*Hippocamelus*) in the Andes (Merkt 1987; Barquez *et al.* 1991), and a deer (*Mazama gouazoubira*) in the Caatinga frequent the rocky habitats, especially during dry weather (Mares *et al.* 1985; T E Lacher Jr, *pers. comm.*).

As the bats, herbivores, microomnivores, and insectivores inhabit the rocks, the habitat becomes increasingly attractive to carnivores, who can forage on the inhabitants of the rocks and adjacent areas. This can be considered a fourth-level effect of the rocks on mammalian species richness. (Of course, carnivores also respond to the rocks for shelter, microclimate, and water, as do other mammals.) In Namibia, for example, the rocks harbor many carnivores, including the leopard *Panthera pardus*, the spotted hyaena, the African wild cat *Felis lybicus*, the black-backed jackal *Canis mesomelas*, and others (Coetzee 1969). In the Caatinga of Brazil, a canid, two mustelids, and several cats frequent the rocky habitat in order to prey on the species of vertebrates and invertebrates that are associated with the rocks. In Argentina, the same families, canids, mustelids, and cats,

frequent the rocky outcrops, many obtaining some of their principal foods from species living in the rocks.

Discussion

The influences of granitic outcrops on patterns of local and regional mammal diversity and ecology are pervasive. In comparing this very similar habitat in quite different environments, it becomes clear that rocks make it possible for a wide variety of rupicolous species to evolve. These species bring with them a high degree of specialized adaptations (and genetic information) to the rupicolous habit that is not present in species in the surrounding habitat. In fact, the rocks provide an important niche component that can only be readily exploited by rock specialists which have developed the special abilities required to live largely or only in rocks (Mares & Lacher 1987). This means that these species, from numerous orders and many families, evolutionarily opt to exploit the rock resource and the microenvironment associated with it. By selecting this evolutionary path, the species are able to persist in regions that would otherwise be more challenging (and support fewer species) due to the generally arid environment (Namibia, the high Andes), or because of the periodic devastating droughts (the Caatinga). Those species that are able to specialize on the rock resource in these regions also appear to move into longer-term ecological strategies, where life spans exceed one year (unlike most boom-and-bust) small mammals, and where microclimatic stability leads to complex morphological, ecological, and behavioral traits to persist in the specialized rock habitat. Once this community of mammals has developed, it becomes possible for species associated with them (e.g. carnivores) also to become regular components of the rock-associated mammal community.

Thus at a local level, granitic outcrops lead to an increase not only in the numbers of species supported in an area, but in higher-order diversity as well. More families and even orders of mammals are able to occur in an area because of the presence of the rocks. Additionally, those species that have evolved to live in rocks are often so specialized that they are endemic to the rocks; no rocks, no species and, in many cases, no genera, families or orders either. This has significant implications for research in conservation biology. Although much attention has been paid to the presence or absence of species as an important measure of a habitat's importance, habitats that contain endemic species (or families or orders) are much more important to maintain than habitats that merely support many species (Mares 1992). Mares made this argument for a comparison between drylands and tropical forests in the Neotropics, but the same argument can be extended to the unique fauna of rocky outcrops as well.

Because rocks open up a series of major new niches in an area, and because to specialize on the rock resource demands a host of unusual adaptations, those species that have taken this evolutionary step become quite different genetically from their nearest relatives. So different, in fact, that their nearest relatives are often in other genera or even families. This is the higher order diversity that was discussed by Mares (1992). When comparing a

tropical and two temperate regions on two different continents, the faunistic evolutionary pattern that appears is similar. Rocks lead to specializations among mammals, which leads to large series of unique adaptations, often quite distinct from their nearest relatives. The rocks also lead to the formation of communities of these specialized mammals that differ greatly in their suites of adaptations from species in the surrounding non-rock habitat. Because the rocks are an ancient habitat and have likely impelled this evolutionary process to begin long ago, rock specialists are phylogenetically unique as well, and the degree of endemism is high at the species level, and at higher taxonomic levels. This results in faunas that contain a great deal of unique genetic material in areas that are quite limited geographically. These should be areas of intense conservation interest. These influences are apparent at both the local and regional level. Indeed, it would be interesting to compare the contribution of rock-dwelling mammals to global diversity not only at the species level, but at levels above the species. Initial indications are that the contribution of rock-piles to global mammal diversity would be quite high indeed.

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Plants of Western Australian granite outcrops

S D Hopper¹, A P Brown² & N G Marchant³

¹Kings Park and Botanic Garden, West Perth WA 6005
email: steveh@kpbg.wa.gov.au

²Western Australian Threatened Species & Communities Unit,
Department of Conservation and Land Management, PO Box 51, Wanneroo WA 6065
email: andrewbr@calm.wa.gov.au

³Western Australian Herbarium, Department of Conservation and Land Management,
PO Box 104, Como WA 6152

Abstract

Outcropping granite rocks in Western Australia span a considerable climatic range, from the mediterranean south-west to inland desert and northern arid subtropics and tropics. At least 1320, and possibly 2000, plant taxa occur on Western Australian granite outcrops. Outcrop plant life is most diverse in the South West Botanical Province, with individual outcrops having up to 200 species, including many endemics not found in surrounding habitats. Species richness and local endemism declines with increasing aridity, to the point where Kimberley and Pilbara outcrops show little discontinuity in species from the surrounding landscape matrix. Outcrops are dominated by woody and herbaceous perennials, especially of the Myrtaceae, Orchidaceae, and Mimosaceae, and have an unusually rich diversity of annuals (Asteraceae, Stylidiaceae, Poaceae, Amaranthaceae *etc.*) compared with the flora as a whole. An unusual life form is found in resurrection plants capable of extreme desiccation and rehydration (*e.g.* *Borya*, *Cheilanthes*). Among woody perennials, bird pollination is frequent, and some outcrops harbour a high proportion of obligate seeder species due to the refuge from fire provided by bare rock barriers. The diversity of microhabitats and soil moisture regimes on outcrops has enabled the persistence of species beyond their main range in the face of climatic fluctuations. It has also facilitated the evolution of many endemics in the south-west. Major threatening processes facing outcrop plant communities include weed invasion, grazing by stock and feral animals, too-frequent fire, clearing, loss of shrub layer, salinity, and dieback. Conservation of these rich rare habitats needs the support of local communities.

Introduction

Western Australia is the largest Australian State, extending 2 391 km north-south and 1 621 km east-west, and occupying 2 525 500 km², or about a third of the nation. Climates range from temperate and mediterranean in the south-west to the monsoonal tropics in the extreme north, with arid conditions prevailing over much of the State from the Nullarbor Plain north through the inland deserts to the north-west Pilbara and Kimberley regions.

Most of the State is a plateau 300-600 m above sea level, with the highest point (Mt Meharry) only 1 251 m. Western Australia's numerous granite inselbergs and outcrops, consequently, are significant landscape features, even though most emerge less than 100 m above surrounding terrain.

Granite (or granitoid) rocks are mainly found on the Yilgarn and Pilbara Cratons, which together occupy about a third of the State's landmass, and along adjacent south coastal and Kimberley orogens (Myers 1997). The outcrops thus span a considerable climatic range, from the mediterranean south-west to inland desert and northern arid subtropics and tropics.

Western Australian outcrops vary in area from about

one tenth of a hectare to many hectares. While most are clearly isolated and disjunct, sometimes separated from the next outcrop by tens of kilometres, others are part of extensive inselberg systems covering several square kilometres (*e.g.* outcrop systems in Cape Le Grand, Porongurups and Cape Arid National Parks on the south coast, at Oudabunna Station near Paynes Find, and at Woodstock Station in the Pilbara). Peak Charles, 100 km north-west of Esperance, stands highest above surrounding country among the State's inselbergs, reaching 500 m from a low plain.

While the Kimberley, Pilbara and desert granites are in regions with depauperate floras not unlike those of much of tropical and arid Australia, the granite of the Yilgarn Craton underlies one of the world's regions richest in plant life, the South West Botanical Province (Marchant 1973; Hopper 1979, 1992; Beard 1980, 1981, 1990). As many as 8000 vascular plant species occur in this region, with about 75% endemism. Consequently, the botanical exploration of south-western inselbergs has been particularly rewarding, and much remains to be done.

Here, we provide an overview of current knowledge of plant life on Western Australian granite outcrops. Our aim was to compile a baseline, including a preliminary list of plants (vascular and cryptogam) collected from Western Australian outcrops, and a list of key references, to inform future research and provide a context for more specific studies. We conclude with some thoughts on the

conservation of this special component of Western Australian plant life.

Botanical Exploration

Western Australian granite outcrops have been important to aboriginal people ever since they occupied the land, but little has been documented of this long-standing relationship (Bindon 1997). Recorded European knowledge of granite outcrop plants in the State commenced with Archibald Menzies, surgeon and naturalist aboard the *HMS Discovery*, under the command of Captain George Vancouver. The *Discovery* was anchored in King George's Sound from September 28 to October 11, 1791.

Menzies made a "copious collection of ... vegetable productions, principally the genus *Banksia*, which are here very numerous" from various sites onshore in the vicinity of present-day Albany (Maiden 1909). Given the prominence of granite headlands, hills and islands at Albany, Menzies undoubtedly collected from them, but details are difficult to trace.

European botanists first named granite outcrop plants from Western Australia in 1800. The Frenchman Jacques J H de Labillardiere was naturalist on Admiral Bruny d'Entrecasteaux's expedition to Australia, which sought refuge from a storm near the modern town of Esperance over the period 9-17 December 1792. Labillardiere's specimens included a plant he named in 1800 as *Eucalyptus cornuta*, collected from the granite Observatory Island on 13 December 1792. *E. cornuta* occupies the apron and deeper soil pockets on granite outcrops throughout the Esperance area and adjacent islands, extending westwards to the Cape Naturaliste area (Fig 1).

Labillardiere named other granite outcrop plants from the expedition, including the bizarre genus *Borya* (Fig 4), a pincushion lily and resurrection plant, named in 1805 and typified by the species *B. nitida* which occurs on shallow soils on outcrops along the south coast from Albany to east of Esperance.

Robert Brown, on the expedition to circumnavigate Australia led by Matthew Flinders in the *Investigator*, anchored at King George's Sound on December 8, 1801, and collected extensively until January 5, 1802. Between January 10-18, the expedition also explored and collected near Esperance, landing at Lucky Bay (in the present-day Cape Le Grand National Park) for five days, and on islands in the Recherche Archipelago. Brown (1810) also named many granite outcrop plants, including another species of *Borya* (*B. spaherocephala*) that occurs with *B. nitida* on several south coast outcrops.

The arrival of James Drummond at the Swan River with Captain Stirling's colonising party on the *Parmelia* in 1829 heralded a major advance in knowledge of the south-west's flora, including that of granite outcrops (Erickson 1969). Drummond, a Scot and keen nurseryman with an excellent eye for new taxa, collected widely throughout the forests and present day wheatbelt, his specimens destined for subscribers in Great Britain and Europe. He was followed by many others up to modern times. Beard (1981) provides a useful historical review. The floral wealth of the south-west is such that significant numbers of new taxa

continue to be discovered and described each year (Green 1985; Hopper 1992), including granite outcrop endemics.

The ecology and biogeography of Western Australian granite outcrop plants were observed by the earliest collectors, but drew specific mention by the plant geographer Ludwig Diels (1906), who noted the "dwarflike" vegetation. Smith (1962) provided an account of the vegetation of the granite Porongurup Range, and many others have mentioned granite outcrop plants in broader vegetation surveys in the south-west (e.g. Beard 1981; Newbey & Hnatiuk 1985; Newbey *et al.* 1995; Wardell Johnson & Williams 1996; Brooker & Margules 1996).

Main (1967) gave a delightful account of the natural history of Yorkrakine Rock through an annual cycle. Marchant (in Erickson *et al.* 1973) summarised botanical features of south-western outcrops in an essay for a general readership.

Schweinfurth (1978) described the vegetation of exposed granite headlands along the south coast, while Abbott & Watson (1978) and Abbott (1980) explored these headlands and adjacent islands in greater detail, showing the flora of most islands had a depauperate subset of that found onshore, and displayed little endemism nor genetic differentiation from mainland populations.

Hopper (1981) highlighted the importance of winter-flowering woody perennials as a nectar resource used by a diversity of honeyeaters in the central wheatbelt (Fig 3). Pate & Dixon (1982) gave a comprehensive account of the biology of tuberous and cormous plants, including many found on granite.

Ornduff (1987) documented the flora of herbfields including, and centrewards from, the *Borya* zone on nine outcrops near Perth and Hyden. Burgman (1987) sampled five outcrops inland from Esperance and explored aspects of rarity in granite communities. Hopper *et al.* (1990) illustrated 29 endangered endemics of granite outcrops and highlighted conservation issues. Pignatti & Pignatti (1994) reported on herbfields from shallow seasonally wet soils on a selection of south-west outcrops. Ohlemüller (1997) documented plants in shallow soil depressions on 26 outcrops throughout the south-west and goldfields.

In parallel with these ecological investigations, genetic studies of Western Australian granite outcrop plants were pioneered by James (1965), who's penetrating work on the herb *Isotoma petraea* (Lobeliaceae) has become a classic in the literature on plant evolution (Bussell & James 1997). Studies on the population genetics of endemic granite outcrop eucalypts have also provided useful insights into the evolution of highly fragmented small populations (Moran and Hopper 1983; Sampson *et al.* 1988). The breeding systems of granite outcrop endemics have been documented for *Villarsia* (Menyanthaceae; Ornduff 1986, 1996) and *Anthocercis gracilis* (Solanaceae; Stace 1995).

Sampling Methods

Rather than laboriously search the increasing number of botanical publications that include plant taxa recorded

on Western Australian granite outcrops, we compiled the plant list from specimens housed in the Western Australian Herbarium. The database WAHERB stores full label details of 413 000 specimens of vascular plants and cryptogams collected throughout the State, and afforded an opportunity to list those taxa for which habitat details on labels included the words "granite outcrop". Initial trials indicated that searching on "granite" or "granitic" alone picked up too many taxa that occupied regions underlain by granite rock, but favoured deep soils well removed from rock outcrops.

In our list, taxa are mainly species, but infraspecific subspecies, varieties and forms, together with hybrids, are all counted. This ensures that all named plant biodiversity is included, and allows for discrepancies in assigning rank among taxonomists.

The above approach to listing plant taxa was based on an understanding that most authors involved in botanical survey of Western Australian granite outcrops have collected voucher specimens and deposited them in the Western Australian Herbarium (e.g. Ornduff 1987; Burgman 1987; Hopper 1981; Hopper *et al.* 1990; Hopper & Brown, *unpublished orchid research*; Newbey & Hnatiuk 1985; Newbey *et al.* 1995). In addition, as an independent check, the senior author has compiled field herbaria in notebooks for *ca* 150 outcrops throughout Western Australia over the past two decades. Most outcrops sampled occur in the South West Botanical Province (e.g. Fig 1) and adjacent pastoral region, while a few have been examined in the Pilbara (e.g. Fig 2) and Kimberley.

Precisely defining the boundaries of a granite outcrop is difficult, especially for mobile components of the biota (Main 1997). However, the sedentary nature of adult plants, especially perennials, affords a reliable and measurable biological indicator of the limits of the outcrop system.

In fieldwork, we have used the distribution of plants that are locally endemic to outcrops to define the extent of outcrop communities sampled. Thus, all species centrewards from the outermost individuals of granite outcrop local endemics were included as present on an outcrop. This approach ensures that all endemics are sampled, but has the effect of picking up some species from surrounding deeper soils that do not extend onto soil pockets on the outcrop itself. Other authors have restricted their sampling to such soil pockets (e.g. Houle 1990; Porembski *et al.* 1995; Ohlemuller 1997), or only to herbfields (e.g. Ornduff 1987). Experience showed that perennial vegetation fringing the base of Western Australian outcrops had to be sampled to ensure a comprehensive inventory (see below).

We followed Newbey and Hnatiuk (1985) and Newbey *et al.* (1995) in collecting on random walks stratified by microhabitat rather than within quadrats *i.e.* the *random stratified walk* technique. A comparison of the senior author's data with the quadrat-based data of Burgman (1987) for Mt Ney inland from Esperance showed that four 5 m x 5 m quadrats spaced at 25 m intervals on NE scree slope and sheet rock yielded 61 taxa, whereas 192 taxa were documented through random stratified walks covering cardinal compass points.

Microhabitats recognised and deliberately searched

for on random stratified walks included bare rock, cryptogamic crusts, gnammas (rock pools or weather pits, seasonal and permanent), soil-filled crevices, caves/tafoni/shade of boulders or exfoliated slabs, herbfields on shallow well-drained soil, herbfields on shallow seasonally waterlogged soil (ephemeral flush vegetation), shrublands and woodlands on deep well-drained soil, shrublands, woodlands and forests on deep seasonally waterlogged soil, permanent springs, major watercourses, and salt lakes.

Floristics

A total of 1320 Western Australian granite outcrop plant taxa were represented and labelled as such in the collections of the Western Australian Herbarium in May 1996 (Appendix 1). Of these, 1097 taxa (83.0%) were described, 94 (7.1%) were undescribed but well-delimited with manuscript names, and 129 (9.9%) were of uncertain taxonomic delimitation. Only 4 (0.3%) were hybrids, well below the proportion (4%) estimated for the whole WA flora (Hopper 1995). The list includes 11 macrofungi, 34 lichens, 46 mosses, 9 liverworts, 9 ferns, 7 fern allies, 2 cycads, 2 conifers, and 1200 angiosperms (284 monocotyledons, 916 dicotyledons).

While these statistics provide a useful baseline, it is pertinent to note that sampling of most cryptogam groups is poor. For example, we recorded only 34 lichens with vouchered granite outcrop specimens for the whole of WA, whereas Pigott & Sage (1997) list 36 lichen taxa for Yilliminning Rock alone. Macrofungi undoubtedly are orders of magnitude more diverse than presently known: The moss flora is comparatively better documented at the species level (Stoneburner *et al.* 1993; Stoneburner & Wyatt 1996), but much more collecting is needed to fill in knowledge of distribution and ecology.

Some confidence may be placed in the list of vascular plant taxa, which accounts for 1220 (92.4%) of the total of 1320. Based on our knowledge of rock outcrop floras across the State, the majority of south-western vascular plant taxa on granite outcrops are listed. However, some conspicuous omissions of taxa that are common (e.g. *Hakea petiolaris*, *Corymbia calophylla*), uncommon (e.g. *Grevillea magnifica*, *Phylloglossum drummondii* and *Isoetes drummondii*) and rare (e.g. *Drummondita hassellii* var *longifolia*, *Hibbertia bracteosa*, *Villarsia calthifolia*, *Pleurophascum occidentale*) indicate that revision upwards is required. Moreover, a comparison of the list of 187 taxa for Yilliminning Rock near Narrogin (Pigott & Sage 1997) with Appendix 1 shows that 78 Yilliminning taxa (42%) are not present in our list for the State. This discrepancy would be even more so for northern outcrops. For example, absent from the present list are the dominant spinifex hummock grasses on granite outcrops (*Triodia* spp), as well as common lemon grasses (*Cymbopogon* spp), and scattered but widespread subtropical woody shrubs and small trees such as *Terminalia canescens*. It would be no surprise to us, consequently, if the number of vascular plant taxa on Western Australian granite outcrops approached 2000 in the future.

In the present list, major vascular plant families include the Myrtaceae (162 taxa), Orchidaceae (159), Mimosaceae

(82), Asteraceae (72), Papilionaceae (66), Proteaceae (54), and Stylidiaceae (33). Genera richest in taxa on granite outcrops include *Acacia* (82 taxa), *Caladenia* (70), *Eucalyptus* (44), *Stylidium* (28), *Melaleuca* (26), *Grevillea* (25), *Drosera* (21), *Verticordia* (20), *Eremophila* (18) and *Thelymitra* (16).

Thus, woody perennial shrubs and trees of myrtles, wattles, peas and Proteaceae are taxon-rich on WA granite outcrops, reflecting trends in the flora as a whole (Green 1985; Hopper *et al.* 1996). However, the granite woody perennials are depauperate in Epacridaceae, which is rich in other habitats. The granite outcrop flora is clearly divergent from the flora at large in the unusually high taxon richness of groups such as the tuberous perennial terrestrials (orchids, sundews, lilies), and herbaceous, often annual, daisies and triggerplants.

Systematic sampling of shallow-soil herbfields on south-western outcrops by Ornduff (1987) and Ohlemüller (1997) yields a useful comparison with our data on herbaceous families. Ornduff recorded 160 taxa belonging to 37 families (he didn't sample Orchidaceae for conservation reasons), of which the largest were Asteraceae, Poaceae, Liliaceae *sens. lat.*, and Stylidiaceae. Ohlemüller recorded 134 species from 42 families, with the largest being Asteraceae, Orchidaceae, Poaceae, Apiaceae, Stylidiaceae and Centrolepidaceae.

Major herbaceous families in our list are Orchidaceae (Fig 5), Asteraceae, Stylidiaceae, Anthericaceae (or Liliaceae *sens. lat.*), Poaceae, Droseraceae, Cyperaceae, Goodeniaceae, Amaranthaceae and Centrolepidaceae. The Amaranthaceae is a family richest in the north of Western Australia, so it is not surprising that Ornduff (1987) and Ohlemüller (1997) found it to be depauperate in their south-west study areas. Orchidaceae undoubtedly emerges as the most taxon-rich herbaceous family in our list because two of us (SH and AB) have made a detailed and prolonged study of granite outcrop orchids, and found that repeat surveys over different seasons and years are needed to develop comprehensive orchid inventories for individual rocks. Other differences between our ranking and those of Ornduff (1987) and Ohlemüller (1997) are minor. This general concordance suggests that major trends and statistics for the vascular plants in Appendix 1 are accurate, at least for south-west outcrops.

Plants of Special Interest

Granite outcrop habitats have elicited remarkable parallel evolution in many plants and animals (Porembski *et al.* 1997; Wyatt 1997; Mares 1997). The combination of high solar radiation, rapid runoff of rainfall, and shallow soils on a rocky substrate provide microhabitats of accentuated seasonal and diurnal stresses. Conditions may vary over a few metres from cool permanently moist shaded caves with water seepage to drought-afflicted shallow soils and rock surfaces fully exposed to all the elements.

Few organisms can tolerate the harshest of these rock-surface habitats, which tend to be occupied by cryptogamic crusts of cosmopolitan cyanobacteria, lichens and mosses such as *Grimmia laevigata*. Western Australian outcrops conform to this trend. However, on

south-west outcrops experiencing high rainfall, moss cushions become prominent, with the luxuriant brown carpets of *Breutelia affinis* and the verdant green *Campylopus bicolor* and *C. australis* noteworthy.

Coping with seasonal or unpredictable drought is, undoubtedly, the most significant survival strategy faced by granite outcrop plants. Among Western Australian herbaceous perennials on outcrops, pincushion lilies (*Borya* spp, Boryaceae) are abundant and remarkable in their capacity as resurrection plants (Gaff 1981) to withstand desiccation to less than 5% of normal leaf moisture content, turning orange in the process, and rehydrating to normal green leaves within a day of rainfall (Fig 4). There are at least six species of *Borya* in the South West Botanical Province (*B. sphaerocephala* is a variable taxon awaiting detailed study and possible subdivision). These plants do not extend to the Pilbara outcrops. Other resurrection plants commonly seen on WA granites include the rock ferns *Cheilanthes* spp and *Pleurosorus rutifolius*.

Persisting underground as a tuber during drought is a common strategy among Western Australian granite outcrop herbs in the south-west and adjacent pastoral regions, especially lilioids (e.g. *Wurmbea* spp, Colchicaceae), orchids (*Caladenia*, *Thelymitra*, *Pterostylis*, *Diuris*, *Prasophyllum*) and sundews (*Drosera*), as well as the unusual fern ally *Phylloglossum* (Pate & Dixon 1982). On northern outcrops, tuberous Cyperaceae tend to occupy this niche.

Succulence is not prominent in the Western Australian granite outcrop perennial floras, but has evolved in a few taxonomically-unrelated species e.g. *Spiculaea ciliata* (Orchidaceae; Fig 5), *Carpobrotus* spp (Aizoaceae). Some perennial shrubs of south coast granites have unusually thick leaves (e.g. *Hakea clavata*, Proteaceae; *Anthocercis viscosa*, Solanaceae), and at least one has tuberous roots (*Calothamnus tuberosus*, Myrtaceae). Sclerophyllous leaves characterise the vast majority of woody perennials found on granite outcrops, as well as in the Western Australian flora at large.

The graminoid habit has evolved in several unrelated groups in the south-west, with common perennials forming tussocks including diverse Cyperaceae (especially *Lepidosperma* spp), blind grass (*Stypania* spp, Phormiaceae), the sedge-like grass *Spartochloa scirpoidea* (Poaceae) and lemon grass *Cymbopogon* spp (Poaceae). Desert, Pilbara and Kimberley outcrops are dominated by uniquely Australian hummock grasses with inrolled pungent leaves (*Triodia* spp, Poaceae).

Drought avoidance through an annual life history is a major feature of Western Australian granite herbs in families such as the Asteraceae, Stylidiaceae, Poaceae, Goodeniaceae, Amaranthaceae and Centrolepidaceae. Most of these annuals have relatively small inconspicuous flowers suggestive of inbreeding (Ornduff 1987), but some are brightly coloured and abundant. Most outcrops in southern Western Australia are bedecked with colourful swards of annual triggerplants (*Stylidium*, Stylidiaceae) and everlastings (e.g. *Rhodanthie*, *Waitzia*, Asteraceae) that enliven the herbfields. Succulence is a feature of some annuals, especially those that occupy the dry spectrum of shallow soils (e.g. *Calandrinia* spp, Portulacaceae; *Crassula* spp, Crassulaceae).



1. Coastal granite outcrops east of Albany on Two Peoples Bay Nature Reserve, with *Eucalyptus cornuta* (pale canopy), described in 1800 by French scientific explorer Labillardiere. Photograph by SD Hopper.



2. Granite sheet, boulders and distant inselbergs in the arid Pilbara, Spear Hill, south-west of Marble Bar. Photograph by SD Hopper.



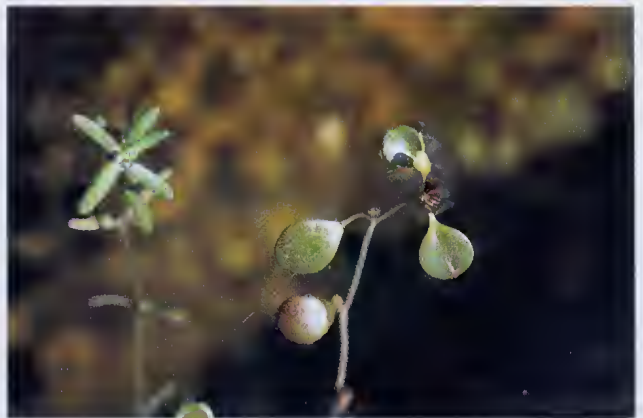
3. Bird-pollinated plants are a feature of south-west Australian granite outcrops - New Holland Honeyeater on *Eucalyptus caesia*, Boyagin Rock, north-west of Pingelly. Photograph by SD Hopper.



4. The resurrection plant, pincushion lily *Borhya constricta*, with leaves 1 cm long desiccated (orange) but rehydrating (green) following rain at the end of summer drought, Chiddarcooping Rock, north-east of Merredin. Photograph by SD Hopper.



5. Terrestrial orchids are the second most species-rich plant family on Western Australian granite outcrops. Here, flowers of the elbow orchid (*Spiculaea ciliata*) 1 cm long splay from the succulent stem that feeds them in early summer, and a male thynnid wasp attempts to copulate with the flower's sexual decoy, an insectiform hinged labellum, Boulder Rock, Brookton Highway. Photograph by BA & AG Wells.



6. Arguably the rarest Western Australian granite outcrop plant, the annual aquatic millfoil *Myriophyllum lapidicola* in full flower (with round floating leaves), and known from just two gnammas (rock pools), alongside the invasive aquatic South African weed, *Crassula natans* var *minus*. Photograph by SD Hopper.

Annuals are also found commonly in seasonally waterlogged shallow soils or ephemeral flush communities (Pignatti & Pignatti 1994). These annuals include species of Centrolepidaceae (*Centrolepis* and *Aphelia*), Apiaceae (*Hydrocotyle*), Juncaginaceae (*Triglochin*), Cyperaceae (*Schoenus*, *Isolepis*, *Cyperus*), Asteraceae (*Quinetia*, *Millotia*, *Rutidosis*, *Siloxerus*, *Toxanthos*, *Hyalosperma*, *Podotheca* etc.) and Stylidiaceae (*Stylidium*, *Levenhookia*).

Deeper soils enable survivorship of woody perennials, of which the largest on Western Australian outcrops include eucalypts (*Eucalyptus* and *Corymbia*, Myrtaceae), wattles (*Acacia*, Mimosaceae), she-oaks (*Allocasuarina*, Casuarinaceae), and rock figs (*Ficus*, Moraceae). A noteworthy feature of the woody perennials is the high proportion of bird-pollinated species (Hopper 1981; Fig 3) in families such as Myrtaceae (e.g. *Eucalyptus*, *Calothamnus*, *Melaleuca*, *Verticordia*), Proteaceae (*Grevillea*, *Hakea*, *Banksia*), Myoporaceae (*Eremophila*), Papilionaceae (*Kennedya*, *Crotolaria*), Viscaceae (*Amyenia*, *Lysiana*) and Sterculiaceae (*Brachychiton*). Also, south-western outcrops have an unusually high number of woody perennials that are obligate seeders - plants that are killed by fire and recruit only from seed. For example, 77% of the perennials in a granite community at Chiddarcooping Nature Reserve north-east of Merredin were obligate seeders (Hopper *et al.*, unpubl.).

Gnammas on Western Australian outcrops have a unique flora comprising annual species of quillworts (*Isoetes*, Isoetaceae), mudmats (*Glossostigma*, Scrophulariaceae), millfoils (*Myriophyllum*, Haloragaceae; Fig 6) and others, including the introduced South African annual *Crassula natans* (Crassulaceae).

Weeds

Ornduff (1987) and Ohlemüller (1997) found that introduced weed species, mainly annuals, comprised 23.7% and 17.0% of the granite herbfield floras sampled respectively. These figures are high compared with the ca 9% that weeds represent of the WA flora as a whole (Green 1985; Keighery 1995). They are even more significant when considered with granite outcrop herbfield floras elsewhere on earth, which have far fewer invasive weeds (Porembski *et al.* 1997; Wyatt 1997).

Weed growth is most pronounced in full sun on outcrops, especially where soil has been disturbed and enriched by rabbit dung or agricultural activity. In these situations, annual grasses such as *Briza maxima*, *Avena fatua* and *Elriharta longifolia* often dominate and replace native annuals throughout much of the south-west. Weeds are rare only where a dense shrub layer or low forest of native woody perennials persist. It is clear that a persistent seed rain of weeds occurs over vast regions of the south-west, as weeds appear in open areas on outcrops where little or no disturbance is evident and native plants dominate.

Hopper (1997) has attributed the high invasibility of disturbed Western Australian plant communities to the absence of major glacial soil stripping as an evolutionary force acting on the flora. Native species are unable to compete against weeds from habitats where soil disturbance is a regular perturbation. Further

experimental study of weeds in granite herbfields could test this hypothesis, and assist attempts at restoration of invaded outcrops.

Biogeography and Endemism

Western Australian granite outcrops display plant biogeographic patterns that mirror that of the whole flora (Hopper 1979, 1992; Hopper *et al.* 1996); species-richness and endemism are pronounced in the transitional rainfall zone (wheatbelt) of the south-west, and attenuate as rainfall decreases through the pastoral country to the deserts, Pilbara and Kimberley. For example, the total number of vascular plant taxa recorded by the senior author and colleagues on a sample of rocks ranged from 142 (Point Matthew, near Augusta) and 201 (Mt Frankland) in the highest rainfall forests, 192 (Mt Ney) and 187 (Yilliminning Rock near Narrogin; Pigott and Sage 1997) in the transitional rainfall zone, to 85 (Daggar Hills, near Yalgoo) in the pastoral zone, and 90 (Moolyella Rocks, east of Marble Bar) and 80 (Spear Hill, west of Marble Bar; Fig 2) in the arid Pilbara.

There are no vascular species shared between northern (Kimberley, Pilbara) outcrops and those in the south-west. Moreover, the northern outcrop floras are virtually identical with that from the matrix of surrounding terrain, save for outcrop specialists like rock figs and rock ferns. Walters & Wyatt (1982) similarly recorded low endemism and little discontinuity between vascular plants on granite outcrops and adjacent landforms of the arid Central Mineral Region of Texas.

In contrast, south-western and adjacent pastoral zone rocks have higher levels of local endemism, especially in the high rainfall forest region where the outcrops present the most striking difference in habitat to the surrounding vegetation matrix (e.g. Wardell Johnson & Williams 1996; Brooker & Margules 1996).

Biogeographical relationships of outcrop floras across the south-west are under ongoing study by the senior author. As a precursor, Hopper & Brown (*unpublished*) documented the distribution of 126 orchid taxa on 41 outcrops ranging from the highest rainfall forests through the transitional zone wheatbelt to the arid zone. Each rock outcrop was treated as a site in a classification of the orchid data.

The study highlighted a number of significant trends. A primary division occurred between the 15 rocks found in the forested High Rainfall Zone (>800 mm *p.a.*) and the rest ranging from the Transitional Rainfall Zone of the wheatbelt into the Arid Zone. Subsequent divisions established as much difference among forest rocks as among the wheatbelt/arid rocks, even though the forest rocks were confined to a much smaller area. Moreover, remarkably, closely adjacent rocks were widely separated in the classification, indicating significant differences in their orchids (e.g. 10.3 km Rock and 10.9 km Rock of Ornduff's (1987), separated by just 600 m of jarrah forest on Albany Highway). Conversely, rocks separated geographically often had similar orchid floras (e.g. Boyagin Rock and Pingaring Rock on the western and eastern sides of the south-central wheatbelt respectively).

These patterns suggest significant barriers to orchid

Table 1

Lists of Western Australian orchid taxa that occur on granite outcrops.

All taxa		
<i>Caladenia attingens</i> subsp <i>attingens</i> ms	<i>Caladenia voigtii</i> ms	<i>Pterostylis aspera</i>
<i>Caladenia attingens</i> subsp <i>gracillima</i> ms	<i>Corybas recurvus</i>	<i>Pterostylis barbata</i>
<i>Caladenia brevisura</i> ms	<i>Cyanicula amplexans</i> ms	<i>Pterostylis elegantissima</i>
<i>Caladenia brownii</i> ms	<i>Cyanicula ashbyae</i> ms	<i>Pterostylis hamiltonii</i>
<i>Caladenia caesarea</i> subsp <i>maritima</i> ms	<i>Cyanicula caerulea</i> subsp <i>apertala</i> ms	<i>Pterostylis mutica</i>
<i>Caladenia caesarea</i> subsp <i>transiens</i> ms	<i>Cyanicula deformis</i> ms	<i>Pterostylis recurva</i>
<i>Caladenia citrina</i> ms	<i>Cyanicula fragrans</i> ms	<i>Pterostylis roensis</i>
<i>Caladenia denticulata</i>	<i>Cyanicula gemmata</i> ms	<i>Pterostylis sanguinea</i>
<i>Caladenia dimidia</i> ms	<i>Cyanicula sericea</i> ms	<i>Pterostylis sargentii</i>
<i>Caladenia discoidea</i>	<i>Cyrtostylis huegelii</i>	<i>Pterostylis scabra</i>
<i>Caladenia douthiae</i>	<i>Cyrtostylis robusta</i>	<i>Pterostylis vittata</i>
<i>Caladenia exstans</i> ms	<i>Diuris aff longifolia</i>	<i>Pyrorchis nigricans</i>
<i>Caladenia falcata</i>	<i>Diuris brumalis</i>	<i>Spiculaea ciliata</i>
<i>Caladenia filifera</i>	<i>Diuris conspicillata</i>	<i>Thelymitra aff holmsii</i>
<i>Caladenia flaccida</i> subsp <i>flaccida</i> ms	<i>Diuris laevis</i>	<i>Thelymitra aff longifolia</i>
<i>Caladenia flaccida</i> subsp <i>pulchra</i> ms	<i>Diuris laxiflora</i>	<i>Thelymitra aff nuda</i>
<i>Caladenia flava</i> subsp <i>flava</i> ms	<i>Diuris longifolia</i>	<i>Thelymitra aff pauciflora</i>
<i>Caladenia flava</i> subsp <i>maculata</i> ms	<i>Diuris maculata</i>	<i>Thelymitra antennifera</i>
<i>Caladenia flava</i> subsp <i>sylvestris</i> ms	<i>Diuris picta</i>	<i>Thelymitra benthamiana</i>
<i>Caladenia footeana</i> ms	<i>Diuris pulchella</i>	<i>Thelymitra crinita</i>
<i>Caladenia granitiora</i> ms	<i>Diuris recurva</i>	<i>Thelymitra cucullata</i>
<i>Caladenia lieberleana</i> ms	<i>Diuris setacea</i>	<i>Thelymitra aff dedmaniarum</i>
<i>Caladenia hirta</i> subsp <i>rosea</i> ms	<i>Drakonorchis barbarossa</i> ms	<i>Thelymitra flexuosa</i>
<i>Caladenia hoffmanii</i> subsp <i>graniticola</i> ms	<i>Drakonorchis drakeoides</i> ms	<i>Thelymitra macrophylla</i>
<i>Caladenia incensa</i> ms	<i>Drakonorchis mesocera</i> ms	<i>Thelymitra spiralis</i>
<i>Caladenia incrassata</i> ms	<i>Elythranthera brunonis</i>	
<i>Caladenia infundibularis</i>	<i>Elythranthera emarginata</i>	Taxa that predominantly occur on granite outcrops
<i>Caladenia integra</i>	<i>Eriochilus dilatatus</i> subsp <i>dilatatus</i> ms	<i>Caladenia caesarea</i> subsp <i>maritima</i> ms
<i>Caladenia latifolia</i>	<i>Eriochilus dilatatus</i> subsp <i>multiflorus</i> ms	<i>Caladenia exstans</i> ms
<i>Caladenia lobata</i>	<i>Eriochilus dilatatus</i> subsp <i>undulatus</i> ms	<i>Caladenia granitiora</i> ms
<i>Caladenia longicauda</i> subsp <i>clivicola</i> ms	<i>Eriochilus helonemos</i> ms	<i>Caladenia hoffmanii</i> subsp <i>graniticola</i> ms
<i>Caladenia longicauda</i> subsp <i>eminens</i> ms	<i>Eriochilus pulchellus</i> ms	<i>Caladenia integra</i>
<i>Caladenia longicauda</i> subsp <i>longicauda</i> ms	<i>Eriochilus scaber</i>	<i>Caladenia longicauda</i> subsp <i>clivicola</i> ms
<i>Caladenia longicauda</i> subsp <i>rigidula</i> ms	<i>Genoplesium nigricans</i>	<i>Caladenia longicauda</i> subsp <i>rigidula</i> ms
<i>Caladenia longiclavata</i>	<i>Leptoceras menziesii</i>	<i>Caladenia multiclavia</i>
<i>Caladenia macrostylis</i>	<i>Lyperanthus serratus</i>	<i>Caladenia nivalis</i>
<i>Caladenia marginata</i>	<i>Microtis aff parviflora</i>	<i>Caladenia remota</i> subsp <i>remota</i> ms
<i>Caladenia microchila</i> ms	<i>Microtis atrata</i>	<i>Cyanicula ashbyae</i> ms
<i>Caladenia multiclavia</i>	<i>Microtis brownii</i>	<i>Cyanicula fragrans</i> ms
<i>Caladenia nivalis</i> ms	<i>Microtis eremaea</i>	<i>Diuris conspicillata</i>
<i>Caladenia pachychila</i> ms	<i>Microtis graniticola</i>	<i>Diuris picta</i>
<i>Caladenia pholcoidea</i> ms	<i>Microtis media</i> subsp <i>eremicola</i>	<i>Diuris pulchella</i>
<i>Caladenia polychroma</i> ms	<i>Microtis media</i> subsp <i>media</i>	<i>Eriochilus pulchellus</i> ms
<i>Caladenia radialis</i>	<i>Monadenia bracteata</i>	<i>Microtis eremaea</i>
<i>Caladenia reptans</i> subsp <i>impensa</i> ms	<i>Paracaleana nigrata</i>	<i>Microtis graniticola</i>
<i>Caladenia reptans</i> subsp <i>reptans</i> ms	<i>Paracaleana triens</i> ms	<i>Microtis media</i> subsp <i>eremicola</i>
<i>Caladenia rhomboidiformis</i>	<i>Prasophyllum aff parvifolium</i>	<i>Spiculaea ciliata</i>
<i>Caladenia roei</i>	<i>Prasophyllum brownii</i>	<i>Thelymitra aff nuda</i>
<i>Caladenia saccharata</i>	<i>Prasophyllum cucullatum</i>	<i>Thelymitra aff dedmaniarum</i>
<i>Caladenia serotina</i> ms	<i>Prasophyllum elatum</i>	
<i>Caladenia sigmoidea</i>	<i>Prasophyllum fimbria</i>	
<i>Caladenia splendens</i> ms	<i>Prasophyllum gibbosum</i>	Declared Rare orchid taxa of granite outcrops
<i>Caladenia hiemalis</i> ms	<i>Prasophyllum gracile</i>	<i>Caladenia caesarea</i> subsp <i>maritima</i> ms
<i>Caladenia horistes</i> ms	<i>Prasophyllum parvifolium</i>	<i>Caladenia exstans</i> ms
<i>Caladenia pendens</i> subsp <i>pendens</i> ms	<i>Prasophyllum ringens</i>	<i>Caladenia hoffmanii</i> subsp <i>graniticola</i> ms
<i>Caladenia remota</i> subsp <i>remota</i> ms	<i>Pterostylis aff nana</i>	<i>Caladenia voigtii</i> ms
<i>Caladenia pendens</i> subsp <i>talbotii</i> ms	<i>Pterostylis aff rufa</i>	<i>Thelymitra aff dedmaniarum</i>
	<i>Pterostylis allantoidea</i>	

dispersal, particularly between forest rocks, and high levels of local extinction and stochastic events underlying the presence of orchids on individual rocks in the south-west and adjacent arid zone. There have been dynamic climatic fluctuations across the south-west for several million years as Australia drifted northwards and arid conditions overtook much of central Australia (Hopper

1979; Hopper *et al.* 1996). The diversity of microhabitats on granite outcrops provided refuge for plants adapted to both dry or wet conditions as the surrounding matrix waxed and waned climatically (Marchant 1973; Main 1997). Survivorship in small populations on granite refuges undoubtedly was a matter of chance in the face of such repeated climatic turmoil.

Interestingly, the above conditions of small disjunct outcrop populations undergoing recurrent stresses is predicted as ideal for genetic divergence and speciation (Grant 1981). Is this prediction borne out by studies of Western Australian outcrop plants? Table 1 provides a recently updated list of 141 orchid taxa recorded from Western Australian granite outcrops. Of these, 22 (16%) are more or less endemic. The endemics have geographical ranges from widespread on outcrops throughout the south-west (e.g. *Spiculaea ciliata*; Fig 5) to highly restricted to a few adjacent outcrops less than 10 km apart (e.g. *Caladenia caesarea* subsp. *maritima*, *Thelymitra* aff. *dedmaniarum*).

In terms of evolutionary origins, these endemics display at least three patterns (Hopper and Brown, unpublished);

- relictual, with no obvious close relatives and therefore likely to have been on granites for a long period of time (e.g. *Spiculaea ciliata*, a monotypic genus);
- derived by speciation from allopatric congeners of habitats other than granite (e.g. *C. granitora*, from coastal granites east of Albany, sister species to *C. infundibularis* of western high rainfall forests and coastal heaths; *C. hoffmanii* subsp. *graniticola*, of east central wheatbelt outcrops, sister to *C. hoffmanii* subsp. *hoffmanii* of lateritic loams well to the north-west in the Northampton region); and
- derived by speciation from allopatric congeners of other granite outcrops (e.g. *C. exstans*, from outcrops east of Esperance, sister to *C. integra* of western wheatbelt outcrops).

Thus, the orchid data do indeed support the hypothesis that conditions on south-west granite outcrops have facilitated genetic divergence and speciation. Genetic studies of a few other granite taxa lend further support, e.g. the herb *Isotoma petraea* (Bussell & James 1997), and eucalypts endemic to granite (Hopper & Burgman 1983; Sampson *et al.* 1988). Clearly, more work along these lines is needed.

There is a large number of granite endemics in south-western Australia, especially among the perennials that dominate the woody vegetation and herbfields. We have already shown that 16% of orchids on outcrops are endemic. For eucalypts, around 24% are endemic (Hopper, unpublished). The level of endemism for the whole granite outcrop flora is difficult to determine without more penetrating research, but there is no doubt that south-western Australia has higher levels than any other system documented (e.g. Walters & Wyatt 1982; Porembski *et al.* 1995, 1997).

The refugial opportunities offered by south-west granite outcrops are also evident in species that have highly disjunct outliers well removed from the main geographical distribution. These include populations on wet outcrop sites in much lower rainfall areas than the main species' stand (e.g. the Jilakin Rock stand of jarrah *Eucalyptus marginata*, the Twine Rock stand of *E. wandoo*, and the Kuendar stand of *E. rudis*). Conversely, arid-adapted species penetrate high rainfall areas on dry north-facing slopes of granites (e.g. populations of *Eucalyptus drummondii* west of Margaret River).

Conservation

Granite outcrops occupy a very small proportion of most Western Australian landscapes in which they occur. Especially in the south-west, the outcrop plant communities are, therefore, by definition, rare, and likely to contain rare species.

Hopper *et al.* (1990) found that endangered granite outcrop plants numbered 29 (12.2%) of the 238 plants declared in 1989 as Rare Flora under the Wildlife Conservation Act. These endangered plants ranged from large mallees (e.g. *Eucalyptus crucis* subsp. *crucis*) and small trees (*Acacia denticulosa*, *Banksia verticillata*), through compact shrubs (e.g. *Drummondia hasselii* var. *longifolia*, *Verticordia staminosa*) and climbers (*Kenedia beckxiana*, *K. macrophylla*) to diminutive herbs (*Tribonanthes purpurea*) and annual aquatics (*Myriophyllum petraeum*). While some endangered taxa have several populations spread across a number of disjunct outcrops, some are confined to very few localities (e.g. *Myriophyllum lapidicola*, known from just two gnammas). Accidental destruction of such populations could be catastrophic. Conservation in the wild in such cases needs to be backed up by off-site activities such as germplasm storage and artificial propagation (underway at Kings Park and Botanic Garden for *M. lapidicola* and other critically endangered granite endemics; Dixon 1994).

Apart from endangered species, the diverse communities on south-western granite outcrops are noteworthy in the rapidity with which they change within and between rocks. They are complex, ever-changing, and rare in their own right.

While many granite outcrops have been spared direct clearing due to their unsuitability for agriculture, and some are included within conservation reserves, most face threatening processes that need management if the native biota is to persist. Such processes include replacement or damage by invasive weeds, feral animals, grazing, inappropriate fire regimes, clearing, loss of shrub layer, salinity and dieback disease. We have briefly addressed the issue of weeds above, and highlighted the importance of maintaining undisturbed soil and dense shrub layers to control weeds effectively. Such restoration activities require an ongoing presence and commitment to a given outcrop. Local communities are vital in this context.

Western Australians are fortunate in being custodians of a unique and diverse suite of granite outcrop plants. We hope that this brief review will stimulate others to study and conserve what is a remarkable heritage.

Acknowledgements: To all those colleagues who helped with field work, discussion and ideas, our sincere thanks. L Sage assisted with the analysis of granite orchid biogeography. R Wyatt and R Ornduff hosted SH on sabbatical in the USA in 1990, and greatly facilitated development of an international perspective on granite outcrop plants. S Porembski has recently broadened this international perspective. We are grateful for their interest and ideas.

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Appendix 1

Alphabetical list of Western Australian plants (vascular and cryptogams combined) represented by specimens in the Western Australian Herbarium and for which habitat descriptions on labels included the words "granite outcrop".

List is current to 28 May 1996, from the WAHERB database of 413 000 specimens collected from all habitats throughout W A. Nomenclature follows Green (1985) and subsequent amendments included in the Western Australian Herbarium's WACENSUS database. Taxa are listed alphabetically by generic, specific and infraspecific names, with entry concluded by family name. Numbers are those assigned to vascular plant families as in Green (1985). Taxa whose family names are preceded by a letter rather than a number are cryptogams as follows: B - moss (bryophyte); H - liverwort (hepatic); L - lichen; F - macrofungus. Uncertainty as to taxonomic delimitation is given by *aff*, *sp*, *?*, "unsorted", *sens. lat.*, or phrase name (e.g. *Form 'n'*, or "*walyahmoningensis*"). Well-delimited but unpublished taxa are identified by *ms* (for manuscript name). Full authorship of all names, published and unpublished, is given in Green (1985) and subsequent amendments included in WACENSUS.

<i>Acacia acuphylla</i> 163 Mimosaceae	<i>Acacia jennerae</i> 163 Mimosaceae
<i>Acacia acutaria</i> 163 Mimosaceae	<i>Acacia jibberdingensis</i> 163 Mimosaceae
<i>Acacia acuminata</i> subsp <i>acuminata</i> ms 163 Mimosaceae	<i>Acacia lasiocalyx</i> 163 Mimosaceae
<i>Acacia acutata</i> 163 Mimosaceae	<i>Acacia leptopetala</i> 163 Mimosaceae
<i>Acacia aff cyperophylla</i> 163 Mimosaceae	<i>Acacia leptostachya</i> 163 Mimosaceae
<i>Acacia aff rhodophloia</i> 163 Mimosaceae	<i>Acacia ligulata</i> 163 Mimosaceae
<i>Acacia andrewsii</i> 163 Mimosaceae	<i>Acacia linophylla</i> 163 Mimosaceae
<i>Acacia aneura</i> var <i>aneura</i> 163 Mimosaceae	<i>Acacia littorea</i> 163 Mimosaceae
<i>Acacia aphylla</i> 163 Mimosaceae	<i>Acacia lysisphloia</i> 163 Mimosaceae
<i>Acacia applanata</i> 163 Mimosaceae	<i>Acacia mirinthophora</i> 163 Mimosaceae
<i>Acacia assimilis</i> subsp <i>assimilis</i> 163 Mimosaceae	<i>Acacia merrallii</i> 163 Mimosaceae
<i>Acacia ayersiana</i> var <i>latifolia</i> 163 Mimosaceae	<i>Acacia microbotrya</i> 163 Mimosaceae
<i>Acacia browniana</i> var <i>browniana</i> (typical variant) 163 Mimosaceae	<i>Acacia monticola</i> 163 Mimosaceae
<i>Acacia browniana</i> var <i>obscura</i> 163 Mimosaceae	<i>Acacia multisiliqua</i> 163 Mimosaceae
<i>Acacia cochlearis</i> 163 Mimosaceae	<i>Acacia myrtifolia</i> 163 Mimosaceae
<i>Acacia conniana</i> 163 Mimosaceae	<i>Acacia olgana</i> 163 Mimosaceae
<i>Acacia constablei</i> 163 Mimosaceae	<i>Acacia prami</i> 163 Mimosaceae
<i>Acacia coolgardiensis</i> subsp <i>coolgardiensis</i> 163 Mimosaceae	<i>Acacia pravifolia</i> 163 Mimosaceae
<i>Acacia coolgardiensis</i> subsp <i>effusa</i> (Pedunculate variant) 163 Mimosaceae	<i>Acacia pulchella</i> subsp <i>pulchella</i> 163 Mimosaceae
<i>Acacia costiniana</i> 163 Mimosaceae	<i>Acacia pulchella</i> var <i>goadbyi</i> 163 Mimosaceae
<i>Acacia cowaniana</i> 163 Mimosaceae	<i>Acacia puncticulata</i> ms 163 Mimosaceae
<i>Acacia cracentis</i> ms 163 Mimosaceae	<i>Acacia ramulosa</i> 163 Mimosaceae
<i>Acacia crenulata</i> ms 163 Mimosaceae	<i>Acacia redolens</i> 163 Mimosaceae
<i>Acacia cuneifolia</i> ms 163 Mimosaceae	<i>Acacia restiacea</i> 163 Mimosaceae
<i>Acacia cyclops</i> 163 Mimosaceae	<i>Acacia rigens</i> 163 Mimosaceae
<i>Acacia denticulosa</i> 163 Mimosaceae	<i>Acacia saligna</i> 163 Mimosaceae
<i>Acacia drummondii</i> subsp <i>elegans</i> Porongurup variant (RJ Cumms ms) 163 Mimosaceae	<i>Acacia scleroclada</i> 163 Mimosaceae
<i>Acacia ephedroides</i> 163 Mimosaceae	<i>Acacia sessilisipica</i> 163 Mimosaceae
<i>Acacia ericifolia</i> 163 Mimosaceae	<i>Acacia sp</i> 163 Mimosaceae
<i>Acacia extensa</i> 163 Mimosaceae	<i>Acacia sp</i> P58 (BR Maslin 3625) 163 Mimosaceae
<i>Acacia fauntleroyi</i> 163 Mimosaceae	<i>Acacia sp</i> P94 (JS Beard 6178) 163 Mimosaceae
<i>Acacia flavipila</i> var <i>flavipila</i> 163 Mimosaceae	<i>Acacia stenoptera</i> 163 Mimosaceae
<i>Acacia graniticola</i> ms 163 Mimosaceae	<i>Acacia stowardii</i> 163 Mimosaceae
<i>Acacia hastulata</i> 163 Mimosaceae	<i>Acacia subaerulea</i> 163 Mimosaceae
<i>Acacia hemiteles</i> 163 Mimosaceae	<i>Acacia subflexuosa</i> subsp <i>subflexuosa</i> 163 Mimosaceae
<i>Acacia heteroclita</i> subsp <i>heteroclita</i> ms 163 Mimosaceae	<i>Acacia tarculensis</i> 163 Mimosaceae
<i>Acacia heteroclita</i> subsp <i>valida</i> ms 163 Mimosaceae	<i>Acacia tetragonophylla</i> 163 Mimosaceae
<i>Acacia huegelii</i> 163 Mimosaceae	<i>Acacia trachycarpa</i> 163 Mimosaceae

- Acacia tratmaniana* 163 Mimosaceae
Acacia trigonophylla 163 Mimosaceae
Acacia triptycha 163 Mimosaceae
Acacia urophylla 163 Mimosaceae
Acacia verrucula 163 Mimosaceae
Acacia viscidifolia 163 Mimosaceae
Acacia willdenowiana 163 Mimosaceae
Acacia ? *glaucescens* 163 Mimosaceae
Acacia ? *quadrangulata* 163 Mimosaceae
Acacia Sect *Pluri* (*microneurae*, *terete*) 163 Mimosaceae
Acarospora citrini L. *Acarosporaceae*
Acaulon integrifolium B. *Pottiaceae*
Actinobole oldfieldiana 345 *Asteraceae*
Actinotus leucocephalus 281 *Apiaceae*
Adenanthos obovatus 090 *Proteaceae*
Agaricus sp. F. *Agaricaceae*
Agonis hypericifolia 273 *Myrtaceae*
Agonis linearifolia 273 *Myrtaceae*
Agonis marginata 273 *Myrtaceae*
Agonis parviceps 273 *Myrtaceae*
Agrostocrinum scabrum 054F *Anthericaceae*
Aira cupaniana 031 *Poaceae*
Allocasuarina campestris 070 *Casuarinaceae*
Allocasuarina decussata 070 *Casuarinaceae*
Allocasuarina erichlamys subsp. *grossa* 070 *Casuarinaceae*
Allocasuarina huegeliana 070 *Casuarinaceae*
Allocasuarina humilis 070 *Casuarinaceae*
Allocasuarina thuyoides 070 *Casuarinaceae*
Allocasuarina trichodon 070 *Casuarinaceae*
Alyogyne hakeifolia 221 *Malvaceae*
Alyogyne huegelii var. *huegelii* ms 221 *Malvaceae*
Alyogyne huegelii var. *araya* ms 221 *Malvaceae*
Alyogyne pinoniana 221 *Malvaceae*
Amanita sp. F. *Amanitaceae*
Amaranthus mitchellii 106 *Amaranthaceae*
Amaranthus pallidiflorus 106 *Amaranthaceae*
Amaranthus sp. (*Silent Grove*) RJC 6532 106 *Amaranthaceae*
Amperea simulans 185 *Euphorbiaceae*
Anapilopogon caricinus 031 *Poaceae*
Anemone gibberula var. *tatei* 097 *Loranthaceae*
Anagallis arvensis 293 *Primulaceae*
Anarthrus prolifera 039 *Restionaceae*
Andersonia aff. *auriculata* 288 *Epacridaceae*
Andersonia aff. *leimanniana* 288 *Epacridaceae*
Andersonia aristata 288 *Epacridaceae*
Andersonia leimanniana 288 *Epacridaceae*
Andersonia parvifolia 288 *Epacridaceae*
Andersonia sp. 288 *Epacridaceae*
Andersonia sprengeloides 288 *Epacridaceae*
Angianthus tomentosus 345 *Asteraceae*
Anthocercis anisantha subsp. *anisantha* 315 *Solanaceae*
Anthocercis genistoides 315 *Solanaceae*
Anthocercis gracilis 315 *Solanaceae*
Anthocercis littorea 315 *Solanaceae*
Anthocercis viscosa subsp. *caudata* 315 *Solanaceae*
Anthocercis viscosa subsp. *viscosa* 315 *Solanaceae*
Anthurus sp. F. *Clathraceae*
Aphelia brizula 040 *Centrolepidaceae*
Aphelia cyperoides 040 *Centrolepidaceae*
Aphelia nutans 040 *Centrolepidaceae*
Aristida contorta 031 *Poaceae*
Arthropodium curvipes 054F *Anthericaceae*
Arthropodium dyeri 054F *Anthericaceae*
Asplenium aethiopicum 011E *Aspleniaceae*
Asplenium flabellifolium 011E *Aspleniaceae*
Astartea ambigua 273 *Myrtaceae*
Astartea fascicularis 273 *Myrtaceae*
Astartea sp. Mt Johnston (AR Annel 5645) 273 *Myrtaceae*
Asterella drummondii H. *Hepaticae*
Asterolasia pallida subsp. "unsorted" 175 *Rutaceae*
Astroloma ciliatum 288 *Epacridaceae*
Astroloma epacridis 288 *Epacridaceae*
Astroloma pallidum 288 *Epacridaceae*
Astroloma prostratum 288 *Epacridaceae*
Astroloma serratifolium 288 *Epacridaceae*
Astroloma sp. 288 *Epacridaceae*
Baeckea "walyahmoningenensis" 273 *Myrtaceae*
Baeckea behrii 273 *Myrtaceae*
Baeckea camphorosmae 273 *Myrtaceae*
Baeckea crispiflora 273 *Myrtaceae*
Baeckea crispiflora ms 273 *Myrtaceae*
Baeckea maidenii 273 *Myrtaceae*
Baeckea margarethae 273 *Myrtaceae*
Baeckea margarethae ms 273 *Myrtaceae*
Baeckea polyandra 273 *Myrtaceae*
Baeckea recurva ms 273 *Myrtaceae*
Baeckea sp. *Paynes Find* (S Patrick 1095) 273 *Myrtaceae*
Baeckea tenuiramea 273 *Myrtaceae*
Baeckea tetragona 273 *Myrtaceae*
Banksia seminuda subsp. *remanans* 090 *Proteaceae*
Banksia verticillata 090 *Proteaceae*
Barbula calycina B. *Pottiaceae*
Barbula crinita B. *Pottiaceae*
Bartsia trixago 316 *Scrophulariaceae*
Beaufortia empetrifolia 273 *Myrtaceae*
Beaufortia incana 273 *Myrtaceae*
Beaufortia schaueri 273 *Myrtaceae*
Blennospora drummondii 345 *Asteraceae*
Boronia albiflora 175 *Rutaceae*
Boronia algida 175 *Rutaceae*
Boronia busselliana 175 *Rutaceae*
Boronia coerulescens subsp. "unsorted" 175 *Rutaceae*
Boronia crassifolia 175 *Rutaceae*
Boronia crenulata var. "unsorted" 175 *Rutaceae*
Boronia crenulata var. *crenulata* 175 *Rutaceae*
Boronia defoliata 175 *Rutaceae*
Boronia gracilipes 175 *Rutaceae*
Boronia inornata subsp. *inornata* 175 *Rutaceae*
Boronia sp. 175 *Rutaceae*
Boronia subsessilis 175 *Rutaceae*
Boronia tetrandra 175 *Rutaceae*
Borya constricta 054F *Anthericaceae*
Borya constricta F. *Anthericaceae*
Borya laciniata 054F *Anthericaceae*
Borya longiscapa 054F *Anthericaceae*
Borya mitida 054F *Anthericaceae*
Borya scopuloides 054F *Anthericaceae*
Borya sphaerocephala 054F *Anthericaceae*
Borya sphaerocephala sens. lat. 054F *Anthericaceae*
Bossiaea dentata 165 *Papilionaceae*
Bossiaea eriocarpa 165 *Papilionaceae*
Bossiaea linophylla 165 *Papilionaceae*
Brachychiton grandiflorus 223 *Sterculiaceae*
Brachychiton gregori 223 *Sterculiaceae*
Brachymenium preissianum B. *Bryaceae*
Brachyscome ciliaris 345 *Asteraceae*
Brachyscome iberidifolia 345 *Asteraceae*
Brachyscome perpusilla 345 *Asteraceae*
Brachyscome sp. 345 *Asteraceae*
Breutelia affinis B. *Bartramiaceae*
Briza maxima 031 *Poaceae*
Briza minor 031 *Poaceae*
Bromus rubens 031 *Poaceae*
Bruchia brevipes B. *Dicranaceae*
Bryum argenteum B. *Bryaceae*
Bryum billardieri B. *Bryaceae*
Bryum caespitium B. *Bryaceae*
Bryum campulothecium B. *Bryaceae*
Bryum capillare B. *Bryaceae*
Bryum cheilii B. *Bryaceae*
Bryum chrysoneuron B. *Bryaceae*
Bryum dichotomum B. *Bryaceae*
Bryum pachytheca B. *Bryaceae*
Bryum sp. B. *Catchside* B. *Bryaceae*
Bryum torquescens B. *Bryaceae*
Bulbine semibarbuta 054G *Asphodelaceae*
Burchardia multiflora 054J *Colchicaceae*
Bursaria occidentalis 152 *Pittosporaceae*
Caesia micrantha 054F *Anthericaceae*
Caladenia attingens subsp. *attingens* ms 066 *Orchidaceae*
Caladenia attingens subsp. *gracillima* ms 066 *Orchidaceae*
Caladenia breviflora ms 066 *Orchidaceae*
Caladenia brownii ms 066 *Orchidaceae*
Caladenia caesarea subsp. *maritima* ms 066 *Orchidaceae*
Caladenia caesarea subsp. *transiens* ms 066 *Orchidaceae*
Caladenia citrina ms 066 *Orchidaceae*
Caladenia denticulata 066 *Orchidaceae*
Caladenia dilatata dilatata 066 *Orchidaceae*
Caladenia dimidia ms 066 *Orchidaceae*
Caladenia discoides 066 *Orchidaceae*

- Caladenia douthiae* 066 Orchidaceae
Caladenia exstans ms 066 Orchidaceae
Caladenia falcata 066 Orchidaceae
Caladenia filifera 066 Orchidaceae
Caladenia flaccida subsp. *flaccida* ms 066 Orchidaceae
Caladenia flaccida subsp. *pulchra* ms 066 Orchidaceae
Caladenia flava subsp. *flava* ms 066 Orchidaceae
Caladenia flava subsp. *maculata* ms 066 Orchidaceae
Caladenia flava subsp. *sylvestris* ms 066 Orchidaceae
Caladenia footeana ms 066 Orchidaceae
Caladenia granitiora ms 066 Orchidaceae
Caladenia hebeleana ms 066 Orchidaceae
Caladenia hirta subsp. *rosea* ms 066 Orchidaceae
Caladenia hoffmannii subsp. *graniticola* ms 066 Orchidaceae
Caladenia incesa ms 066 Orchidaceae
Caladenia incrassata ms 066 Orchidaceae
Caladenia infundibularis 066 Orchidaceae
Caladenia integra 066 Orchidaceae
Caladenia latifolia 066 Orchidaceae
Caladenia lobata 066 Orchidaceae
Caladenia longicauda subsp. *clivicola* ms 066 Orchidaceae
Caladenia longicauda subsp. *eminens* ms 066 Orchidaceae
Caladenia longicauda subsp. *longicauda* ms 066 Orchidaceae
Caladenia longicauda subsp. *rigidula* ms 066 Orchidaceae
Caladenia longiclavata 066 Orchidaceae
Caladenia macrostylis 066 Orchidaceae
Caladenia marginata 066 Orchidaceae
Caladenia microchila ms 066 Orchidaceae
Caladenia multiclavia 066 Orchidaceae
Caladenia nivalis ms 066 Orchidaceae
Caladenia pachychila ms 066 Orchidaceae
Caladenia pendens ms 066 Orchidaceae
Caladenia pholcoidea ms 066 Orchidaceae
Caladenia polychroma ms 066 Orchidaceae
Caladenia radialis 066 Orchidaceae
Caladenia reptans subsp. *impensa* ms 066 Orchidaceae
Caladenia reptans subsp. *reptans* ms 066 Orchidaceae
Caladenia rhomboidiformis 066 Orchidaceae
Caladenia roei 066 Orchidaceae
Caladenia saccharata 066 Orchidaceae
Caladenia serotina ms 066 Orchidaceae
Caladenia sigmoidea 066 Orchidaceae
Caladenia splendens ms 066 Orchidaceae
Caladenia hiemalis ms 066 Orchidaceae
Caladenia horistes ms 066 Orchidaceae
Caladenia pendens subsp. *pendens* ms 066 Orchidaceae
Caladenia remota subsp. *remota* ms 066 Orchidaceae
Caladenia pendens subsp. *talbotii* ms 066 Orchidaceae
Caladenia roigii ms 066 Orchidaceae
Calandrinia calyptrata 111 Portulacaceae
Calandrinia ptychosperma 111 Portulacaceae
Calectasia grandiflora 054C Dasypogonaceae
Callitriche stagnalis 186 Callitrichaceae
Callitris glaucophylla 018 Cupressaceae
Callitris preissii subsp. "unsorted" 018 Cupressaceae
Calocephalus multiflorus 345 Asteraceae
Calophaea sp. l. Teloschistaceae
Calothamnus quadrifidus var. "unsorted" 273 Myrtaceae
Calothamnus quadrifidus var. *Esperance District* (AE Orchard 1676) 273 Myrtaceae
Calothamnus rupestris 273 Myrtaceae
Calothamnus schaueri 273 Myrtaceae
Calothamnus sp. 273 Myrtaceae
Calothamnus tuberosus 273 Myrtaceae
Calothamnus villosus 273 Myrtaceae
Calycopeplus pauciflorus 185 Euphorbiaceae
Calytrix acutifolia 273 Myrtaceae
Calytrix angulata 273 Myrtaceae
Calytrix decandra 273 Myrtaceae
Calytrix depressa 273 Myrtaceae
Calytrix fraseri 273 Myrtaceae
Calytrix glutinosa 273 Myrtaceae
Calytrix leschenaultii 273 Myrtaceae
Calytrix tetragona 273 Myrtaceae
Campylopus australis B Dicranaceae
Campylopus bicolor B Dicranaceae
Campylopus findersii B Dicranaceae
Campylopus introflexus B Dicranaceae
Carpobrotus aequilaterus 110 Aizoaceae
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Maireana glomerifolia 105 Chenopodiaceae
Malleostemon tuberculatus 273 Myrtaceae
Marsdenia graniticola 305 Asclepiadaceae
Marsilea drummondii 013 Marsileaceae
Melaleuca adnata 273 Myrtaceae
Melaleuca ctenoides 273 Myrtaceae
Melaleuca cuticularis 273 Myrtaceae
Melaleuca diosmyfolia 273 Myrtaceae
Melaleuca eleuterostachya 273 Myrtaceae
Melaleuca elliptica 273 Myrtaceae
Melaleuca eximia ms 273 Myrtaceae
Melaleuca fulgens subsp *fulgens* 273 Myrtaceae

- Melaleuca fulgens* subsp *steadmanii* 273 Myrtaceae
Melaleuca glaberrima 273 Myrtaceae
Melaleuca globifera 273 Myrtaceae
Melaleuca hamulosa 273 Myrtaceae
Melaleuca holosericea 273 Myrtaceae
Melaleuca lasiantha 273 Myrtaceae
Melaleuca laxiflora 273 Myrtaceae
Melaleuca leiocarpa 273 Myrtaceae
Melaleuca macronychia subsp *macronychia* 273 Myrtaceae
Melaleuca pentagona var *subulifolia* 273 Myrtaceae
Melaleuca pulchella 273 Myrtaceae
Melaleuca pungens var "unsorted" 273 Myrtaceae
Melaleuca radula 273 Myrtaceae
Melaleuca scabra 273 Myrtaceae
Melaleuca sp 273 Myrtaceae
Melaleuca uncinata 273 Myrtaceae
Melaleuca urceolaris 273 Myrtaceae
Melaleuca viminea 273 Myrtaceae
Melilotus indicus 165 Papilionaceae
Menegazzia foraminulosa L Hypogymniaceae
Menegazzia subpervusa L Hypogymniaceae
Mentha spicata 313 Lamiaceae
Mesomelaena tetragona 032 Cyperaceae
Micromyrtus serrulata 273 Myrtaceae
Micromyrtus sulphurea 273 Myrtaceae
Microtis aff parviflora 066 Orchidaceae
Microtis atrata 066 Orchidaceae
Microtis brownii 066 Orchidaceae
Microtis media subsp "inland race" 066 Orchidaceae
Microtis media subsp *media* 066 Orchidaceae
Microtis rara 066 Orchidaceae
Millotia depauperata 345 Asteraceae
Millotia myosotidifolia 345 Asteraceae
Millotia tenuifolia var *tenuifolia* 345 Asteraceae
Mirbelia longifolia 165 Papilionaceae
Mirbelia sp 165 Papilionaceae
Mitrasacme nudicaulis 302 Loganiaceae
Mitrasacme sp 302 Loganiaceae
Monadenia bracteata 066 Orchidaceae
Monotaxis grandiflora 185 Euphorbiaceae
Muehlenbeckia adpressa 103 Polygonaceae
Muelleraanthus trifoliolatus 165 Papilionaceae
Mukia maderaspatana 337 Cucurbitaceae
Myriocephalus guerinae 345 Asteraceae
Myriocephalus nudus 345 Asteraceae
Myriocephalus occidentalis 345 Asteraceae
Myriocephalus pygmaeus 345 Asteraceae
Myriophyllum balladoniense 276 Haloragaceae
Myriophyllum lapidicola 276 Haloragaceae
Myriophyllum petraeum 276 Haloragaceae
Myriophyllum sp 276 Haloragaceae
Nelsonia campestris 325 Acanthaceae
Nemcia acuta 165 Papilionaceae
Neofuscelia pulla L. Parmeliaceae
Neurachne alopecuroides 031 Poaceae
Nicotiana caricola 315 Solanaceae
Nicotiana occidentalis subsp *obliqua* 315 Solanaceae
Nicotiana rotundifolia 315 Solanaceae
Olearia aff paucidentata 345 Asteraceae
Olearia algida 345 Asteraceae
Olearia muelleri 345 Asteraceae
Olearia paucidentata 345 Asteraceae
Olearia propinqua 345 Asteraceae
Olearia stuartii 345 Asteraceae
Ompholappula concava 310 Boraginaceae
Opercularia vaginata 331 Rubiaceae
Ophioglossum lusitanicum 005 Ophioglossaceae
Ophioglossum sp 005 Ophioglossaceae
Osteospermum clandestinum 345 Asteraceae
Oudemansiella sp f. Tricholomataceae
Ozothamnus alpinus 345 Asteraceae
Ozothamnus ramosus 345 Asteraceae
Pandorea pandorana 317 Bignoniaceae
Paracaleana nigrita 066 Orchidaceae
Paracaleana triens ms 066 Orchidaceae
Paraserianthes lophantha subsp *lophantha* 163 Mimosaceae
Parentucellia latifolia 316 Scrophulariaceae
Parentucellia viscosa 316 Scrophulariaceae
Parmelia sp L. Parmeliaceae
Paspalidium clementii 031 Poaceae
Patersonia occidentalis 060 Iridaceae
Pelargonium australe 167 Geraniaceae
Pelargonium cf. littorale 167 Geraniaceae
Pelargonium drummondii 167 Geraniaceae
Pelargonium havilae 167 Geraniaceae
Pelargonium sp 167 Geraniaceae
Pentastichis airoides 031 Poaceae
Pericalymnia ellipticum var *floridum* ms 273 Myrtaceae
Persoonia amaliae 090 Proteaceae
Persoonia falcata 090 Proteaceae
Persoonia pentasticha ms 090 Proteaceae
Persoonia quinquerivis 090 Proteaceae
Petalostylis cassioides 164 Caesalpinaceae
Petrophile divaricata 090 Proteaceae
Petrophile squamata 090 Proteaceae
Petrophile striata 090 Proteaceae
Petrorhagia velutina 113 Caryophyllaceae
Phebalium elegans ms 175 Rutaceae
Phebalium filifolium 175 Rutaceae
Phebalium rhytidophyllum 175 Rutaceae
Philoteca langei 175 Rutaceae
Philydrella pygmaea subsp "unsorted" 050 Philydraceae
Philydrella pygmaea subsp *pygmaea* 050 Philydraceae
Phyllangium divergens 302 Loganiaceae
Phyllangium paradoxum ms 302 Loganiaceae
Phyllanthus calycinus 185 Euphorbiaceae
Phyllanthus sp 185 Euphorbiaceae
Pimelea brachyphylla 263 Thymelaeaceae
Pimelea ciliata 263 Thymelaeaceae
Pimelea ferruginea 263 Thymelaeaceae
Pimelea forrestiana 263 Thymelaeaceae
Pimelea graniticola 263 Thymelaeaceae
Pimelea imbricata var *imbricata* 263 Thymelaeaceae
Pimelea imbricata var *pilgera* 263 Thymelaeaceae
Pimelea microcephala subsp *microcephala* 263 Thymelaeaceae
Pimelea preissii 263 Thymelaeaceae
Pimelea sp 263 Thymelaeaceae
Pimelea spiculigera var *thesioides* 263 Thymelaeaceae
Pimelea suaveolens subsp *suaveolens* 263 Thymelaeaceae
Pimelea sulphurea 263 Thymelaeaceae
Pittosporum phylliraeoides 152 Pittosporaceae
Pityrodia dilatata 311A Chloanthaceae
Pityrodia teckiana 311A Chloanthaceae
Pityrodia terminalis 311A Chloanthaceae
Plantago debilis 329 Plantaginaceae
Platysace compressa/filiformis 281 Apiaceae
Platysace compressa 281 Apiaceae
Pleurodium nervosum B Ditrachaceae
Pleurosorus rudifolius 011E Aspleniaceae
Pleurosorus subglandulosus 011E Aspleniaceae
Pleurotus nidiformis F Polyporaceae
Poa annua 031 Poaceae
Poa poriformis 031 Poaceae
Podolepis canescens 345 Asteraceae
Podolepis capillaris 345 Asteraceae
Podolepis lessonii 345 Asteraceae
Podolepis rugata 345 Asteraceae
Podotheca angustifolia 345 Asteraceae
Podotheca wilsonii 345 Asteraceae
Pogonolepis stricta 345 Asteraceae
Polucarpaea breviflora var *gracilis* 113 Caryophyllaceae
Polucarpaea corymbosa var "unsorted" 113 Caryophyllaceae
Polygala orbicularis 183 Polygalaceae
Porana commixta 307 Convolvulaceae
Porana sericea 307 Convolvulaceae
Potha drummondii B Pottiaceae
Prasophyllum aff parvifolium 066 Orchidaceae
Prasophyllum broenii 066 Orchidaceae
Prasophyllum cucullatum 066 Orchidaceae
Prasophyllum elatum 066 Orchidaceae
Prasophyllum fimbria 066 Orchidaceae
Prasophyllum gibbosum 066 Orchidaceae
Prasophyllum gibbosum subsp *gibbosum* 066 Orchidaceae
Prasophyllum gracile 066 Orchidaceae
Prasophyllum parvifolium 066 Orchidaceae
Prasophyllum riugens 066 Orchidaceae
Prasophyllum sp 066 Orchidaceae
Prostanthera baxteri 313 Lamiaceae
Prostanthera campbellii 313 Lamiaceae
Prostanthera carrickiana 313 Lamiaceae

- Prostanthera florifera* 313 Lamiaceae
Prostanthera grylloana 313 Lamiaceae
Prostanthera magnifica 313 Lamiaceae
Prostanthera serpyllifolia subsp *microphylla* 313 Lamiaceae
Prostanthera sp 1 313 Lamiaceae
Prostanthera striatiflora 313 Lamiaceae
Prostanthera verticillaris 313 Lamiaceae
Pterochaeta paniculata 345 Asteraceae
Pterostylis aff uana 066 Orchidaceae
Pterostylis aff rufa 066 Orchidaceae
Pterostylis allantoidea 066 Orchidaceae
Pterostylis aspera 066 Orchidaceae
Pterostylis barbata 066 Orchidaceae
Pterostylis elegantissima 066 Orchidaceae
Pterostylis hamiltonii 066 Orchidaceae
Pterostylis mutica 066 Orchidaceae
Pterostylis recurva 066 Orchidaceae
Pterostylis roensis 066 Orchidaceae
Pterostylis sanguinea 066 Orchidaceae
Pterostylis sargentii 066 Orchidaceae
Pterostylis scabra 066 Orchidaceae
Pterostylis vittata 066 Orchidaceae
Ptilotus corymbosus var *corymbosus* 106 Amaranthaceae
Ptilotus divaricatus var "unsorted" 106 Amaranthaceae
Ptilotus gaudichaudii var "unsorted" 106 Amaranthaceae
Ptilotus gaudichaudii var *parviflorus* 106 Amaranthaceae
Ptilotus humilis var *humilis* 106 Amaranthaceae
Ptilotus incanus var *incanus* 106 Amaranthaceae
Ptilotus obovatus var "unsorted" 106 Amaranthaceae
Ptilotus obovatus var *obovatus* 106 Amaranthaceae
Ptilotus polystachyus forma *rubriflorus* 106 Amaranthaceae
Ptilotus spathulatus forma *spathulatus* 106 Amaranthaceae
Pultenaea elachista 165 Papilionaceae
Pultenaea ericifolia 165 Papilionaceae
Pultenaea obcordata 165 Papilionaceae
Punctelia subrudecta L. Parmeliaceae
Pyrorchis nigricans 066 Orchidaceae
Quinetia urvillei 345 Asteraceae
Quinqueremulus linearis 345 Asteraceae
Ranunculus colonorum 119 Ranunculaceae
Ranunculus sp 119 Ranunculaceae
Restio crispatus 039 Restionaceae
Rhadinanthus euphemiae 175 Rutaceae
Rhagodia eremaea 105 Chenopodiaceae
Rhagodia preissii subsp *preissii* 105 Chenopodiaceae
Rhodanthe battii 345 Asteraceae
Rhodanthe chlorocephala subsp *splendida* 345 Asteraceae
Rhodanthe citrina 345 Asteraceae
Rhodanthe frenchii 345 Asteraceae
Rhodanthe manglesi 345 Asteraceae
Rhodanthe rubella 345 Asteraceae
Rhodanthe spicata 345 Asteraceae
Rhodanthe tietkensii 345 Asteraceae
Riccia crinita H Ricciaceae
Riccia crystallina H Ricciaceae
Riccia lamellosa H Ricciaceae
Riccia limbata H Ricciaceae
Ricinocarpos glaucus 185 Euphorbiaceae
Ricinocarpos rosmarinifolius 185 Euphorbiaceae
Rimelia reticulata L. Parmeliaceae
Rinzia sp 273 Myrtaceae
Rulingia craurophylla 223 Sterculiaceae
Rulingia cygnorum 223 Sterculiaceae
Rulingia kempiana 223 Sterculiaceae
Rulingia luteiflora 223 Sterculiaceae
Russula "small white" (K Syme 633/93) F Russulaceae
Rutidosia multiflora 345 Asteraceae
Samolus repens subsp "unsorted" 293 Primulaceae
Santalum spicatum 092 Santalaceae
Scaevola glandulifera 341 Goodeniaceae
Scaevola spinescens 341 Goodeniaceae
Scaevola thesioides subsp *filifolia* 341 Goodeniaceae
Schizaea sp 006 Schizaeaceae
Schoenia ayersii 345 Asteraceae
Schoenia cassiniana 345 Asteraceae
Schoenus aff odontocarpus 032 Cyperaceae
Schoenus multigumis 032 Cyperaceae
Schoenus odontocarpus (Small typical variant) 032 Cyperaceae
Schoenus sculptus 032 Cyperaceae
Schoenus sp 3 (aff *odontocarpus*) 032 Cyperaceae
Sclerolaena costata 105 Chenopodiaceae
Sclerolaena fusiformis 105 Chenopodiaceae
Scyphocoronis major 345 Asteraceae
Selaginella gracilima 003 Selaginellaceae
Sematophyllum homomallum B Sematophyllaceae
Senecio hispidulus var *hispidulus* 345 Asteraceae
Senecio leucoglossus 345 Asteraceae
Senna artemisioides subsp x *artemisioides* 164 Caesalpiniaceae
Senna artemisioides subsp x *sturtii* 164 Caesalpiniaceae
Senna glutinosa subsp *charlesiana* 164 Caesalpiniaceae
Sida calyxhymenia 221 Malvaceae
Sida hookeriana 221 Malvaceae
Siloxerus filifolius 345 Asteraceae
Siphula coriacea L. Siphulaceae
Sisymbrium irio 138 Brassicaceae
Solanum cleistogamum 315 Solanaceae
Solanum ferocissimum 315 Solanaceae
Solanum lasiophyllum 315 Solanaceae
Solanum lucani 315 Solanaceae
Solanum nummularium 315 Solanaceae
Solanum orbiculatum subsp *orbiculatum* 315 Solanaceae
Solanum phlomoides 315 Solanaceae
Solanum symonii 315 Solanaceae
Sollya heterophylla 152 Pittosporaceae
Sonchus asper sens lat 345 Asteraceae
Spartochloa scirpoidea 031 Poaceae
Spergularia rubra 113 Caryophyllaceae
Sphenotoma capitatum 288 Epacridaceae
Spiculaea ciliata 066 Orchidaceae
Stackhousia monogyna 202 Stackhousiaceae
Stackhousia muricata 202 Stackhousiaceae
Stenanthemum notiale subsp *notiale* 215 Rhamnaceae
Stipa compressa 031 Poaceae
Stipa henupogon 031 Poaceae
Stipa variabilis 031 Poaceae
Stropharia sp F *Strophariaceae*
Stylidium amoenum var "unsorted" 343 Stylidiaceae
Stylidium arenicola 343 Stylidiaceae
Stylidium assimile 343 Stylidiaceae
Stylidium brevicaupum var *brevicaupum* 343 Stylidiaceae
Stylidium brunonianum subsp "unsorted" 343 Stylidiaceae
Stylidium brunonianum subsp *brunonianum* 343 Stylidiaceae
Stylidium bulbiferum var "unsorted" 343 Stylidiaceae
Stylidium caespitosum 343 Stylidiaceae
Stylidium calcaratum 343 Stylidiaceae
Stylidium crassifolium 343 Stylidiaceae
Stylidium despectum 343 Stylidiaceae
Stylidium dichotomum 343 Stylidiaceae
Stylidium dielsianum 343 Stylidiaceae
Stylidium divaricatum 343 Stylidiaceae
Stylidium diversifolium 343 Stylidiaceae
Stylidium ecorne 343 Stylidiaceae
Stylidium emarginatum subsp *emarginatum* 343 Stylidiaceae
Stylidium inundatum 343 Stylidiaceae
Stylidium longibracteatum 343 Stylidiaceae
Stylidium merrallii 343 Stylidiaceae
Stylidium neglectum 343 Stylidiaceae
Stylidium nungarivense 343 Stylidiaceae
Stylidium perpusillum 343 Stylidiaceae
Stylidium pulchellum 343 Stylidiaceae
Stylidium pygmaeum 343 Stylidiaceae
Stylidium sp 343 Stylidiaceae
Stylidium spathulatum subsp "unsorted" 343 Stylidiaceae
Stylidium spathulatum subsp *acuminatum* 343 Stylidiaceae
Stypania glauca 054E Phormiaceae
Swainsona gracilis 165 Papilionaceae
Swainsona sp 165 Papilionaceae
Synaphea sp 090 Proteaceae
Templetonia sulcata 165 Papilionaceae
Tephrosia sp 165 Papilionaceae
Tephrosia sp B *Kimberley Flora* (CA Gardner 7) 165 Papilionaceae
Tetragonia cristata 110 Aizoaceae
Tetrapterum cylindricum B Pottiaceae
Tetraria capillaris 032 Cyperaceae
Tetrathea aff harperi 182 Tremandraceae
Tetrathea deltoides 182 Tremandraceae
Tetrathea hirsuta 182 Tremandraceae
Tetrathea hispidissima 182 Tremandraceae
Tetrathea nuda 182 Tremandraceae
Tetrathea paynterae 182 Tremandraceae

- Thelymitra* SP 066 Orchidaceae
Thelymitra aff *hoelsii* 066 Orchidaceae
Thelymitra aff *longifolia* 066 Orchidaceae
Thelymitra aff *nuda* 066 Orchidaceae
Thelymitra aff *pauciflora* 066 Orchidaceae
Thelymitra antennifera 066 Orchidaceae
Thelymitra benthamiana 066 Orchidaceae
Thelymitra crinita 066 Orchidaceae
Thelymitra cucullata 066 Orchidaceae
Thelymitra dedmaniarum 066 Orchidaceae
Thelymitra flexuosa 066 Orchidaceae
Thelymitra macmillanii 066 Orchidaceae
Thelymitra macrophylla 066 Orchidaceae
Thelymitra nuda 066 Orchidaceae
Thelymitra sp 066 Orchidaceae
Thelymitra sp 066 Orchidaceae
Thelymitra spiralis 066 Orchidaceae
Themeda triandra 031 Poaceae
Thomasia foliosa 223 Sterculiaceae
Thomasia glutinosa var *latifolia* 223 Sterculiaceae
Thomasia grandiflora 223 Sterculiaceae
Thomasia multiflora 223 Sterculiaceae
Thomasia pauciflora 223 Sterculiaceae
Thomasia petalocalyx 223 Sterculiaceae
Thomasia sp 223 Sterculiaceae
Thryptomene australis 273 Myrtaceae
Thryptomene mucronulata 273 Myrtaceae
Thryptomene saxicola 273 Myrtaceae
Thryptomene sp 273 Myrtaceae
Thuidium sparsum var *hastatum* B Thuidiaceae
Thysanotus hookeri L. Cladoniaceae
Thysanotus dichotomus 054F Anthericaceae
Thysanotus manglesianus 054F Anthericaceae
Thysanotus sparteus 054F Anthericaceae
Thysanotus tenellus 054F Anthericaceae
Thysanotus triandrus 054F Anthericaceae
Tinospora smilacina 122 Menispermaceae
Tolpis barbata 345 Asteraceae
Tortula antarctica B Pottiaceae
Tortula princeps B Pottiaceae
Trachymene cyanopetala 281 Apiaceae
Trachymene moorei subsp *Tutanning* (AS George 12867) ms 281 Apiaceae
Trachymene oruata 281 Apiaceae
Trachymene pilosa 281 Apiaceae
Trachymene sp *Pilbara* (RA Saffrey 1117) ms 281 Apiaceae
Tremandra diffusa 182 Tremandraceae
Tremandra stelligera 182 Tremandraceae
Tribonanthes australis 055 Haemodoraceae
Tribonanthes longipetala 055 Haemodoraceae
Tribonanthes purpurea 055 Haemodoraceae
Tribulus terrestris 173 Zygophyllaceae
Trichodesma zeylanicum var "unsorted" 310 Boraginaceae
Tricoryne elatior 054F Anthericaceae
Trifolium dubium 165 Papilionaceae
Triglochin aff *minutissimum* 026 Juncaginaceae
Triglochin calcitrapum subsp *incurvum* ms 026 Juncaginaceae
Triglochin centrocarpum 026 Juncaginaceae
Triglochin minutissimum 026 Juncaginaceae
Triglochin sp 026 Juncaginaceae
Tripogon loliformis 031 Poaceae
Tripterococcus brunonis 202 Stackhousiaceae
Triptilodiscus pygmaeus 345 Asteraceae
Triquetrella papillata B Pottiaceae
Trymalium ledifolium var *rosmarinifolium* 215 Rhamnaceae
Trymalium spatulatum 215 Rhamnaceae
Tylophora sp 305 Asclepiadaceae
Ursinia anthemoides 345 Asteraceae
Usnea confusa L. Parmeliaceae
Usnea inermis L. Usneaceae
Utricularia menziesii 323 Lentibulariaceae
Utricularia multifida 323 Lentibulariaceae
Utricularia violacea 323 Lentibulariaceae
Velleia cycuopotamica 341 Goodeniaceae
Velleia triuervis 341 Goodeniaceae
Verticordia acerosa var *acerosa* 273 Myrtaceae
Verticordia acerosa var *preissii* 273 Myrtaceae
Verticordia brownii 273 Myrtaceae
Verticordia chrysanthella 273 Myrtaceae
Verticordia chrysanthella 273 Myrtaceae
Verticordia endlicheriana var *angustifolia* 273 Myrtaceae
Verticordia habrantha 273 Myrtaceae
Verticordia helmsii 273 Myrtaceae
Verticordia huegelii var *decumbens* 273 Myrtaceae
Verticordia huegelii var *huegelii* 273 Myrtaceae
Verticordia huegelii var *tridens* 273 Myrtaceae
Verticordia minutiflora 273 Myrtaceae
Verticordia penicillaris 273 Myrtaceae
Verticordia pennigera 273 Myrtaceae
Verticordia plumosa 273 Myrtaceae
Verticordia plumosa var *grandiflora* 273 Myrtaceae
Verticordia plumosa var *plumosa* 273 Myrtaceae
Verticordia staminosa subsp *cylindracea* var *cylindracea* 273 Myrtaceae
Verticordia staminosa subsp *cylindracea* var *erecta* 273 Myrtaceae
Verticordia staminosa subsp *staminosa* 273 Myrtaceae
Viminaria juncea 165 Papilionaceae
Vulpia myuros 031 Poaceae
Wahlenbergia preissii 339 Campanulaceae
Waitzia acuminata var *acuminata* 345 Asteraceae
Waitzia nitida 345 Asteraceae
Waitzia podolepis 345 Asteraceae
Waitzia suaveolens var *flava* 345 Asteraceae
Weissia brachycarpa B Pottiaceae
Weissia controversa B Pottiaceae
Weissia rutilans B Pottiaceae
Westringia dampieri 313 Lamiaceae
Wurmbea cernua 054J Colchicaceae
Wurmbea densiflora 054J Colchicaceae
Wurmbea dioica 054J Colchicaceae
Wurmbea dioica subsp *alba* 054J Colchicaceae
Wurmbea murchisoniana 054J Colchicaceae
Wurmbea pygmaea 054J Colchicaceae
Wurmbea tenella 054J Colchicaceae
Xanthoparmelia digitiformis L. Parmeliaceae
Xanthoparmelia hypoleia L. Parmeliaceae
Xanthoparmelia isidigera L. Parmeliaceae
Xanthoparmelia neotinctina L. Parmeliaceae
Xanthoparmelia reptans L. Parmeliaceae
Xanthoparmelia substriatosa L. Parmeliaceae
Xanthoparmelia tasmanica L. Parmeliaceae
Xanthoria parietina L. Teloschistaceae
Xanthosia candida 281 Apiaceae
Xanthosia singuliflora 281 Apiaceae
Xerolirion divaricata 054C Dasygogonaceae

Terrestrial fauna of granite outcrops in Western Australia

P C Withers & D H Edward

Department of Zoology, The University of Western Australia, Nedlands WA 6907
email: pwithers@cyllene.uwa.edu.au

Abstract

In our overview of the terrestrial animals associated with granite outcrops in Western Australia, we document relatively few animals which are known to be restricted to granite outcrops, despite the large area over which granite outcrops occur in Western Australia. The spider *Teyl* and the chironomid fly *Archaeocochilus* are restricted to granite outcrops. Other spiders (e.g. *Rebilus*), some pseudoscorpions (e.g. *Synsphyronus*) and the embiopteran web-spinner (*Notoligotoma*) may be restricted to granite outcrops. No amphibians are restricted to granite outcrops, although many species use them for shelter or breeding, and some species seem to be restricted to the eastern extent of the granites along the south coast of Western Australia. Only four reptiles appear to be restricted to granite outcrops, the dragon (agamid) lizards *Ctenophorus ornatus*, *C. yinnietharra* and *C. rufescens*, and the gecko *Gehyra montium*, but many other species have been recorded from granite outcrops. Birds, being more mobile than other terrestrial vertebrates, range widely and no species are restricted to granites, although many species are found on granite outcrops. No mammals appear to be restricted to granite outcrops, although a number are rock specialists (e.g. rock wallabies *Petrogale* spp, long-tailed dunnart *Sminthopsis longicauda*, rock rats *Zygomys* spp, rock ringtail possum *Pseudocheirus dahli*), and various other species use granite outcrops as well as other habitats. Although relatively few species of terrestrial animals appear to be restricted to granite outcrops, many animals are found in these specialised habitats, and it is clear that granite outcrops are important as a seasonal resource or temporary refuge for the fauna of the surrounding habitats. The fringing apron of granite outcrops is an important site of interaction between granite outcrops and their surrounding habitats, and must be preserved as vigorously as the granite outcrops themselves.

Introduction

One of the objectives of this symposium, and this issue of The Journal of The Royal Society of Western Australia, was to examine and hopefully explain the pattern of distribution of some animals and plants in Western Australia, with respect to the extensive granite outcrops that are a major geological feature of much of the State. Here, we overview the terrestrial animals associated with granite outcrops in Western Australia.

Granite outcrops form a complex part of the varied ecosystems in Western Australia, although they are often perceived as isolated rock forms jutting out of the surrounding landscape. Not only do they form a specialised suite of habitats for animals and plants in their own right (e.g. rock pools, meadows, exfoliating rock sheets, rock crevices) but they also merge with the surrounding habitats and form specialised edge habitats, the fringing apron. Thus, the flora and fauna associated with granite outcrops are not only those species adapted to survive and persist on the granite rock habitats, but include many species from the surrounding habitats that seek temporary or permanent refuge amongst the granite rocks, or on the fringing apron.

Even a cursory examination of published accounts of the fauna identified on granite outcrops reveals that an immense number of animals has been reported to be

associated with granite outcrops on either a temporary or permanent basis (e.g. the Western Australian Museum Biological Survey reports; Lovell 1978; Dell *et al.* 1985; Anon, 1991; Hopper 1981), various unpublished reports of granite rock fauna and flora surveys, field guides to Western Australian animals (e.g. Storr *et al.* 1981, 1983, 1986, 1990; Storr & Johnstone 1985; Tyler *et al.* 1994) and more general guides to Australian animals (e.g. Strahan 1983; Wilson & Knowles 1988; Cogger 1992). This reflects the opportunistic or seasonal activities of many of these animals rather than any predilection or requirement for granite outcrop habitats. Therefore, for practical reasons, the scope of our investigation here has been limited to the terrestrial fauna restricted to granite outcrops in Western Australia.

Distribution of Granites

Granite outcrops are distributed widely throughout Western Australia. Although there does not appear to be a specific map of granite outcrops in Western Australia, the distribution of granite and sandstone landforms clearly indicates a widespread distribution of granite outcrop habitats over much of the western half of Western Australia, and sandstone habitats in northern, eastern and west-central Western Australia (Fig 1; see also Myers, 1997). Much of the western part, particularly the Yilgarn cratonic block, is covered by granite, and there are scattered patches of granite in the East and West Pilbara. There is a pronounced "V"-shaped patch of granite in the Kimberley, and scattered patches of granite

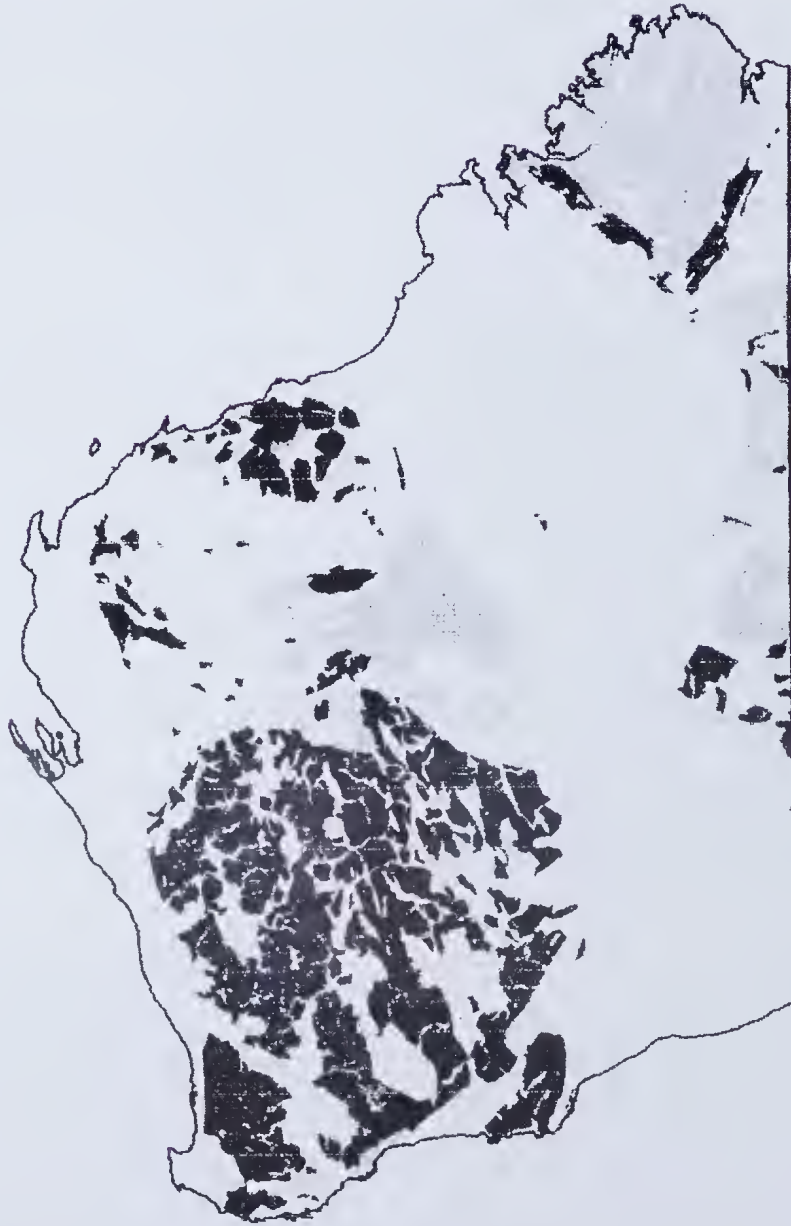


Figure 1. Distribution of granitoid (dark) and sandstone (light) landforms in Western Australia. Redrawn from the Hydrogeological Map of Western Australia, Geological Survey of Western Australia (1989); not shown are other Precambrian and Cambrian landforms (shale, limestone, dolomite, undifferentiated sedimentary, metamorphic, basalt, dolerite, volcanic and gneiss and Phanerozoic sedimentary rocks).

along the eastern border, particularly around the Musgrave Ranges.

The granite outcrops of Western Australia were formed in three major, distinct orogens, representing separate episodes of continental collision (see Myers 1997). The most extensive granite outcrops are part of the Yilgarn Craton, and were formed between 2700 and 2600 million years ago, by the melting of continental crust; these include the Pilbara granites, which are mostly buried by volcanic rocks and the Hamersley banded iron formations. The younger granite outcrops of the Kimberley and Gascoyne regions result from the colliding, about 2000 million years ago, of the Pilbara and Yilgarn continents (Gascoyne region, Capricorn orogen), and others (Kimberley region, Halls Creek and King Leopold orogens). More recently, granite was formed in

the south of Western Australia in two distinct episodes of continental crust collision. The older of these, the Recherche granite, was intruded about 1300 million years ago by deformation of the Mawson Craton (South Australia and East Antarctica) and the West Australian Craton at the Albany-Fraser Orogen. Younger Esperance granite, about 1180 million years old, may be largely derived from another episode of compression between the Mawson and West Australian Cratons. The Musgrave granites formed at about the same time through deformation between the Mawson Craton and the North Australian Craton.

It is clear that the times of formation of these different groups of granite outcrops in Western Australia immensely pre-date the presence of existing species of terrestrial vertebrates and invertebrates, and so current

distributions of terrestrial animals on granite outcrops must reflect relatively recent (in geological time) evolutionary and dispersal patterns rather than relictual isolation of species on the various groups of granites.

Terrestrial Invertebrates

Consideration of the various terrestrial invertebrates indicates that only a few arthropods are known to be restricted to granite outcrops.

The mygalomorph spider *Teyl luculentus* is found in virtually all of the meadows, and also on the fringing apron, of granite outcrops in the wheatbelt and western Goldfields areas of south-western Australia (B York Main, *pers. comm.*). *Teyl* (Fig 2) is an ancient trapdoor spider genus and its distribution appears to be relictual, associated with the wetter, boggy meadows and aprons of granite outcrops; *T. luculentus* is doubtless a complex of species to be described (B York Main, *pers. comm.*). Main (1975) listed various granite rocks as habitats for *T. luculentus*, but some of those records now relate to new species, some restricted to specific rocks, as the genus is being revised; all *Teyl* are restricted to granite outcrops or granite-related habitats (apron, granitic soils; B York Main, *pers. comm.*). *Teyl* aestivates during the dry periods by encasing itself in its sealed burrow. A number of other mygalomorph spiders have been recorded from the fringing apron or outer edge of granite outcrops, including *Kwonkan* sp, *Merredinia damsonoides*, *Aganippe* sp, *Gaius* sp, *Barychelidae* sp, *Chenistonia tepperi* and *Aname diversicolor*, but are not restricted to granite outcrops (B York Main, *pers. comm.*).

The most common and conspicuous spiders of granites in the wheatbelt and goldfields are the large spiders found in vegetation around the granites e.g. the golden orb weaver (*Nephila edulis*), Christmas spider (*Gasteracantha minax*) and huntsman spiders (*Olios* sp). Many spiders are well adapted to living in granite



Figure 2. The burrowing mygalomorph spider *Teyl luculentus* is commonly found in small meadows on granite rocks and the seasonal boggy apron habitats (B York Main).



Figure 3. The pseudoscorpions *Synsphyronus* sp are known from granite outcrops, (D Elford, Western Australian Museum).

outcrops, although not restricted to them, being also found in vegetation and under tree bark. The sparassid huntsman spiders usually live in cracks and crevices of rocks, as well as under loose bark; they have a flattened cephalothorax and abdomen, with legs rotated forwards, making them adept at moving in narrow spaces in rock cracks and between slabs of exfoliating granite. The clubionid and gnaphosid sac spiders, *Rebilus*, *Hemicloea*, *Miturga* and some lycosids are often found under exfoliating granites, as also are redback spiders (*Latrodectus*). The relatively large *Rebilus* is a common spider under the exfoliating granites of the central wheatbelt in Western Australia; it is also found under bark on trees. In the higher rainfall south-western granites, it is replaced by *Miturga*, and in the lower rainfall eastern wheatbelt and goldfields it is replaced by the wolf spider *Pardosa* (Main, 1975). *Rebilus* has a flattened body, like the sparassid huntsman spiders. The dorso-ventrally compressed selenopid spiders are found in rock piles and under bark. Some wolf spiders, and the dysderid spider *Ariadna*, are also found with *Teyl* in the boggy meadows and aprons of granite outcrops. *Ariadna* forms a silk tube, from which radiate silk threads.

Some species of the pseudoscorpion genus *Synsphyronus* (Fig 3) may be restricted to granite outcrops; *S. elegans* Beier is known only from Yorkrakine Hill, *S. leo* Harvey is known only from Lion Island, Recherche Archipelago, and two undescribed species have been collected from other granite outcrops (M Harvey, *pers comm*). However, further collecting is needed to confirm that these species are definitely restricted to granite outcrops, since most species of *Synsphyronus* are found under the bark of trees, in leaf litter, and under other types of rocks (Harvey 1987).

The Embioptera (web-spinners), a small order of insects, are mainly tropical species but some occur in warm temperate climates, like the related termites and earwigs (Ross 1991). These small, slender insects, with a large head and eyes, live in silk tunnels which they weave

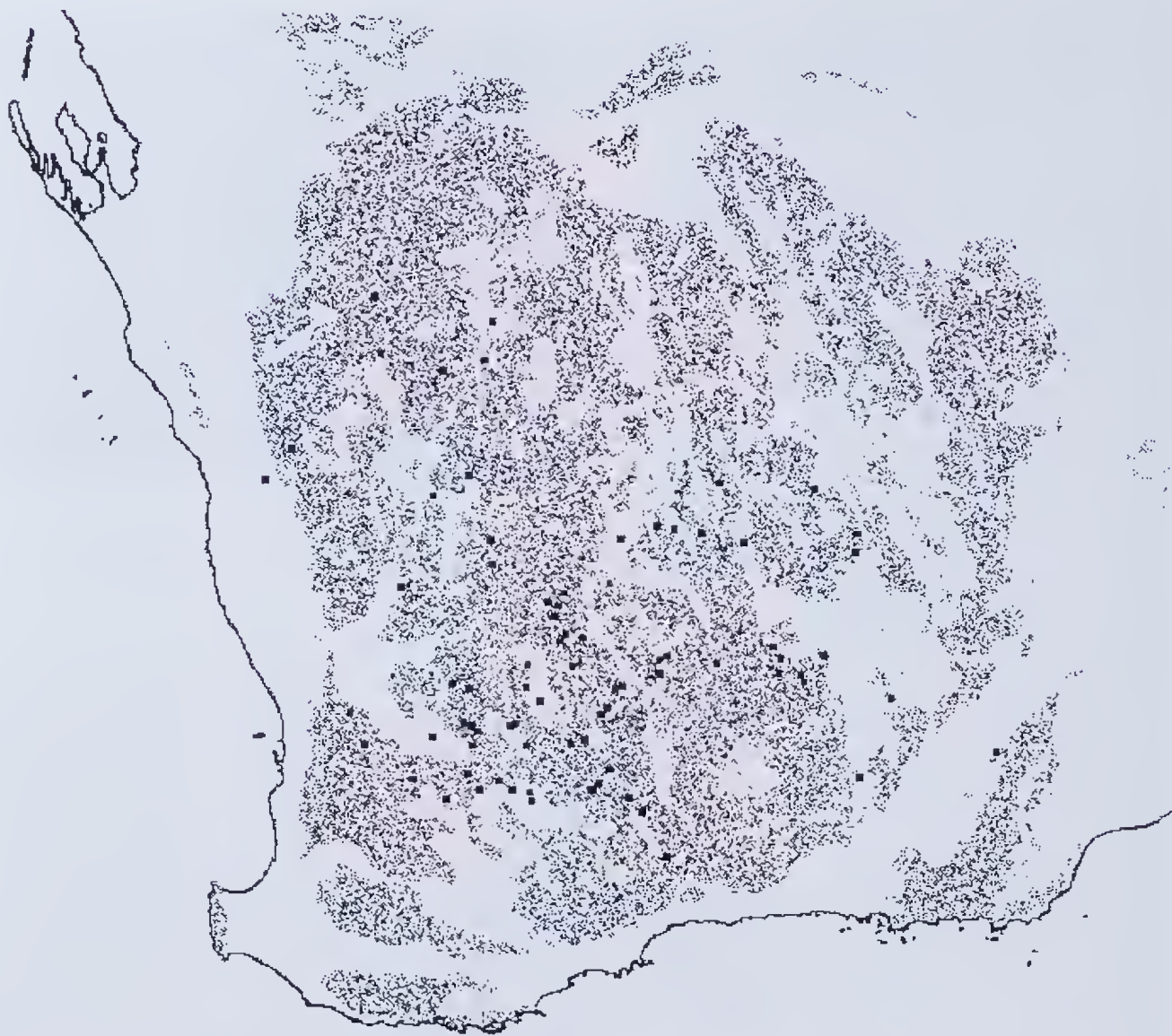


Figure 4. The distribution of *Archaeochlus brundini* and *A. sp. nov.* is restricted to the ancient granite outcrops in Western Australia (AGSO bedrock data, acid/intermediate intrusions; graphed using Arcview by staff of the Western Australian Museum).

using silk glands and spinning glands located on the front tarsi; they feed on vegetation. The embiopteran *Notoligotoma* may be restricted, in part, to granite outcrops. Ross (1991) states that "*Notoligotoma hardyi* and a complex of related species or races occur in south-western Australia, usually on the undersurfaces of exfoliated rock slabs on granitic outcrops of arid regions. In Perth, *N. hardyi* is common in crevices of old board fences in residential areas".

The aquatic invertebrates that occur in pools on granite outcrops are discussed by Bayly (1982, 1997). Another important aquatic habitat on granite outcrops is the temporary streams formed by seepages from the meadows on the outcrops. In these seepages are the larvae of *Archaeochlus*, an ancient genus of chironomid fly. *Archaeochlus* spp are restricted to granite outcrops in south-western Australia (Fig 4) and survive the dry period as a gravid adult female. The genus is also known from temporary streams in the Drakensberg

Escarpment of southern Africa, and provides evidence of a Gondwanan connection between Australia and Africa. The two continental lineages are considered to antedate the breakup of Gondwanaland in the Upper Jurassic and have therefore been separated for a minimum of 120 million years (Cranston *et al.* 1987; Edward 1989).

Terrestrial Vertebrates

As with invertebrates, it is difficult to discern which terrestrial vertebrate species are restricted to granite outcrops, as a very large number of species of amphibians, reptiles, birds and mammals can be found associated with granite outcrops either permanently, temporarily or seasonally. No fishes, amphibians, snakes, birds or mammals are restricted to granite outcrops, but four lizards (three dragons and one gecko) are apparently restricted to granite outcrops (Table 1).

Table 1

Summary of the number of species of frogs, lizards and snakes found in Western Australia, indicating the number of species restricted to granite rocks (g) or rocks in general (r; usually sandstone or limestone). Based on Tyler *et al.* (1994), Storr *et al.* (1981, 1983, 1986, 1990), Wilson & Knowles (1988), and Cogger (1992).

1		9		0		)	
Wilson & Knowles (1988), and Cogger (1992).		<i>Fordonia</i>		1		<i>Achlys</i>	
		<i>Myron</i>		1		<i>Aprasia</i>	
FROGS		Colubridae				<i>Delma</i>	
77 (0g, 5r)		<i>Amphiesma</i>		1		<i>Lialis</i>	
Leptodactylidae		<i>Boiga</i>		1		<i>Pletholax</i>	
<i>Arenophryne</i>		<i>Dendrelaphis</i>		1		<i>Pygopus</i>	
<i>Crinia</i>		Elapidae				Scincidae	
<i>Geocrinia</i>		<i>Acanthophis</i>		3		<i>Bassiana</i>	
<i>Heleioporus</i>		<i>Cryptohis</i>		1		<i>Carlia</i>	
<i>Limnodynastes</i>		<i>Demansia</i>		7		<i>Cryptoblepharus</i>	
<i>Megistolotus</i>		<i>Denisonia</i>		4		<i>Ctenotus</i>	
<i>Metacrinia</i>		<i>Furina</i>		1		<i>Egernia</i>	
<i>Myobatrachus</i>		<i>Notechis</i>		5		<i>Eremiascincus</i>	
<i>Neobatrachus</i>		<i>Oxyuranus</i>		1		<i>Hemiergis</i>	
<i>Notoden</i>		<i>Pseuchis</i>		2		<i>Lerista</i>	
<i>Pseudophryne</i>		<i>Pseudonaja</i>		5		<i>Menetia</i>	
<i>Ranidella</i>		<i>Rhinoplocephalus</i>		6		<i>Morethia</i>	
<i>Uperoleia</i>		<i>Vermicella</i>		11		<i>Notoscincus</i>	
Hylidae		LIZARDS		270 (4g, 25r)		<i>Omolepida</i>	
<i>Cyclorana</i>		Gekkonidae				<i>Proablepharus</i>	
<i>Litoria</i>		<i>Crenadactylus</i>		1		<i>Sphenomorphus</i>	
7		<i>Diplodactylus</i>		28 (2r)		<i>Tiliqua</i>	
18 (3r)		<i>Gehyra</i>		9 (1g, 2r)		Agamidae	
SNAKES		<i>Heteronotia</i>		3 (2r)		<i>Caimanops</i>	
80 (0g, 0r)		<i>Nephruirus</i>		6		<i>Chelosania</i>	
Typhlopidae		<i>Oedura</i>		6 (2r)		<i>Chlamydosaurus</i>	
<i>Raniphytyphlops</i>		<i>Phyllodactylus</i>		1		<i>Ctenophorus</i>	
18		<i>Pseudothecadactylus</i>		1 (1r)		<i>Diporiphora</i>	
Boidae		<i>Rhynchoedura</i>		1		<i>Gemmatophora</i>	
<i>Aspidites</i>		<i>Underwoodisaurus</i>		1		<i>Moloch</i>	
<i>Morelia</i>		Pygopodidae				<i>Pogona</i>	
2						<i>Tympanocryptis</i>	
7						Varanidae	
Acrochordidae						<i>Varanus</i>	
<i>Chersydrus</i>						18 (5r)	
1							
Homalopsidae							
<i>Cerberus</i>							
1							

Amphibians

None of the recorded 77 species of Western Australian amphibians (frogs) appear to be restricted to granite outcrops, based on their distributions or habitats, although a number of species are sometimes associated with rocks (including granites) as either adults or eggs/tadpoles (see Tyler *et al.* 1994). For example, adult treefrogs (*Litoria rubella*) will shelter in cracks in rocks; eggs and tadpoles of frogs, such as the kunapalari frog (*Neobatrachus kunapalari*), are often found in gnammas on granite outcrops, or in ponds around the apron of outcrops.

A notable relationship, however, exists in the close correspondence of the eastern-most extent of granites along the south coast of Western Australia with the eastern-most limit of the distributional range for a number of frogs (L Smith, *pers. comm.*). Examination of the distribution of Western Australian frogs (see Tyler *et al.* 1994) shows a reasonable correspondence for over 10 species with the easternmost extent of the granites at about Israelite Bay (Fig 5), which also coincides with the eastern limit of the south-western winter rainfall zone. This coincidence suggests that these species of frog, although not restricted to granites, might be limited in

the eastern extent of their distribution by the absence of granite outcrops that either directly (as rock pools) or indirectly (as pools formed by run-off from rocks) provide suitable breeding sites elsewhere.

In contrast to no species being restricted to granite rocks, five frog species appear to be restricted to other rock habitats in the Pilbara and Kimberley regions of Western Australia (Table 1). The woodworker frog *Megistolotis lignarius* is always associated with rocks, being found beneath rock piles, on open escarpments or in caves (Tyler *et al.* 1994). The habitat of Douglas' toadlet *Pseudophryne douglasi* is permanent seeps or deep, shaded pools in deep gorges and canyons (Main 1965). Three treefrogs, the cave-dwelling frog *Litoria cavernicola*, Copeland's rock frog *L. copelandi* and the rockhole frog *L. meriana*, are found only near rock pools, caves or streams over rock in the Kimberley region.

Reptiles

Although many lizards and snakes have been collected under exfoliating slabs or rocks on granite outcrops (see Storr *et al.* 1981, 1983, 1986, 1990; Wilson & Knowles 1988; Cogger 1992), only four species of lizards appear to be restricted to granite outcrops.

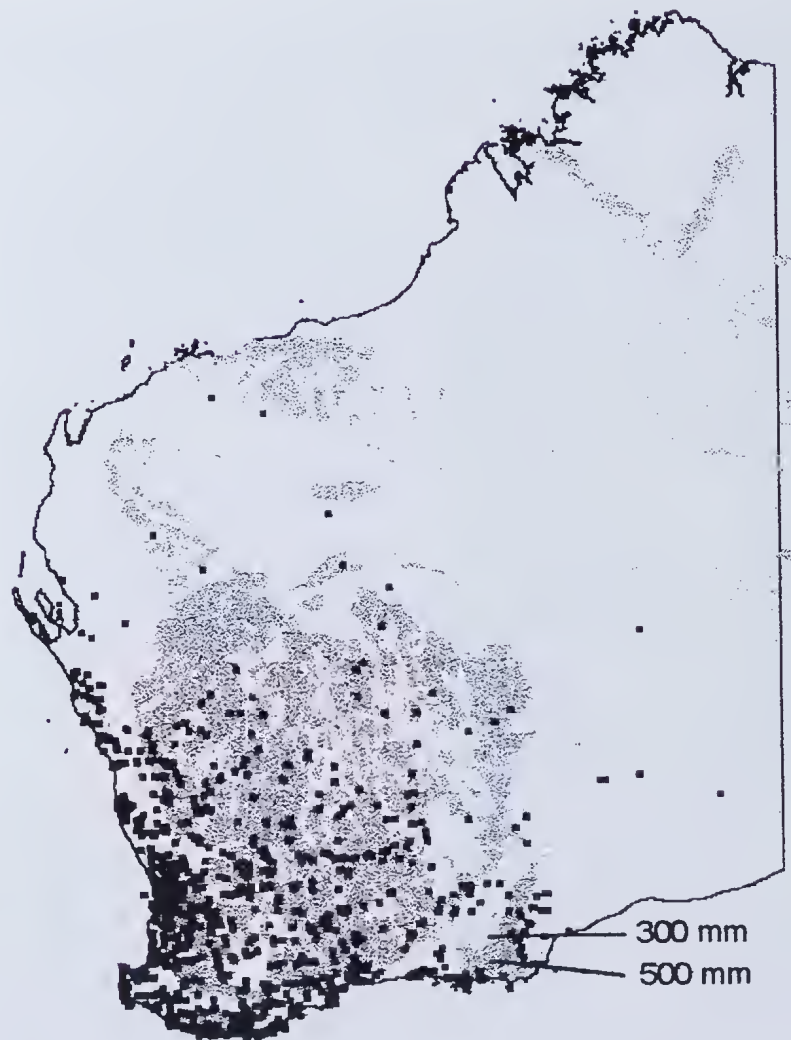


Figure 5. Relationship between eastern distributional limits for 13 species of Western Australian frogs and the eastern extent of granite outcrops; the eastern limits of the south west winter rainfall zone (annual rainfall 300 and 500 mm isohyets) are also indicated. The species of frogs are; *Crinia georgiana*, *Heleioporus eyrei*, *Limnodynastes dorsalis*, *Litoria adelaidensis*, *Litoria cyclorhynchus*, *Myobatrachus gouldii*, *Neobatrachus albipes*, *Neobatrachus kunapalari*, *Neobatrachus pelobatoides*, *Pseudophryne guentheri*, *Pseudophryne occidentalis*, *Ranidella insignifera* and *Ranidella subinsignifera*. Distributional data (total sample size is 6925) from records of the Western Australian Museum; frog localities are plotted over the acid/intermediate intrusions (AGSO bedrock data, acid/intermediate intrusions; graphed using Arcview by staff of the Western Australian Museum).

The most obvious lizards restricted to granite outcrops are some of the *Ctenophorus* dragons. The ornate dragon, *Ctenophorus ornatus*, is commonly found on granite outcrops of the semiarid and subhumid zones of southwestern Western Australia, where it favours expanses of bare rock strewn with exfoliations and loose rocks (Bradshaw 1971). It is restricted to certain granites of the Yilgarn and the Esperance and Recherche regions by cold temperatures and aridity, and does not occur on the Pilbara, Musgrave or Kimberley granites (Fig 6A). Other species of *Ctenophorus* occur in these granite regions, some of which are also restricted to granites. In the Pilbara, the Yinnietharra rock dragon (*C. yinnietharra*) is known only from or near low granite outcrops, and the rusty dragon (*C. rufescens*) is found on granite outcrops in the Musgrave Range region of Western Australia (Fig 6A). In contrast, other saxicolous *Ctenophorus* dragons in the Pilbara, particularly the ring-tailed dragon (*C. caudicinctus*) but also to a lesser extent

the Western netted dragon (*C. reticulatus*), are found more widely on the other rock forms such as volcanic and banded iron formations, as well as granite outcrops.

Only one gecko is apparently restricted to granite outcrops. *Gehyra montium* (Fig 6B) occurs only on the granite outcrops of the Musgrave Range region of east Western Australia, having a similar distribution as the rusty dragon (*C. rufescens*). One other gehyra gecko, the spotted dtella *G. punctata*, is a saxicolous species that is restricted in part to granite rocks, but also occurs on other rock forms (Fig 6B), like the ring-tailed dragon (*C. caudicinctus*). Two diplodactyline geckos, *Diplodactylus wilsoni* and *D. wombeyi*, and *Heteronolia spelea* are rock-dwellers in the Pilbara region. Another wide-spread gehyra gecko, the spotted dtella *G. variegata*, is predominantly arboreal, but in the western part of its range (*i.e.* Western Australia) is both arboreal and saxicolous, under exfoliating rocks on granite outcrops. A similar dichotomy of arboreal and exfoliating granite

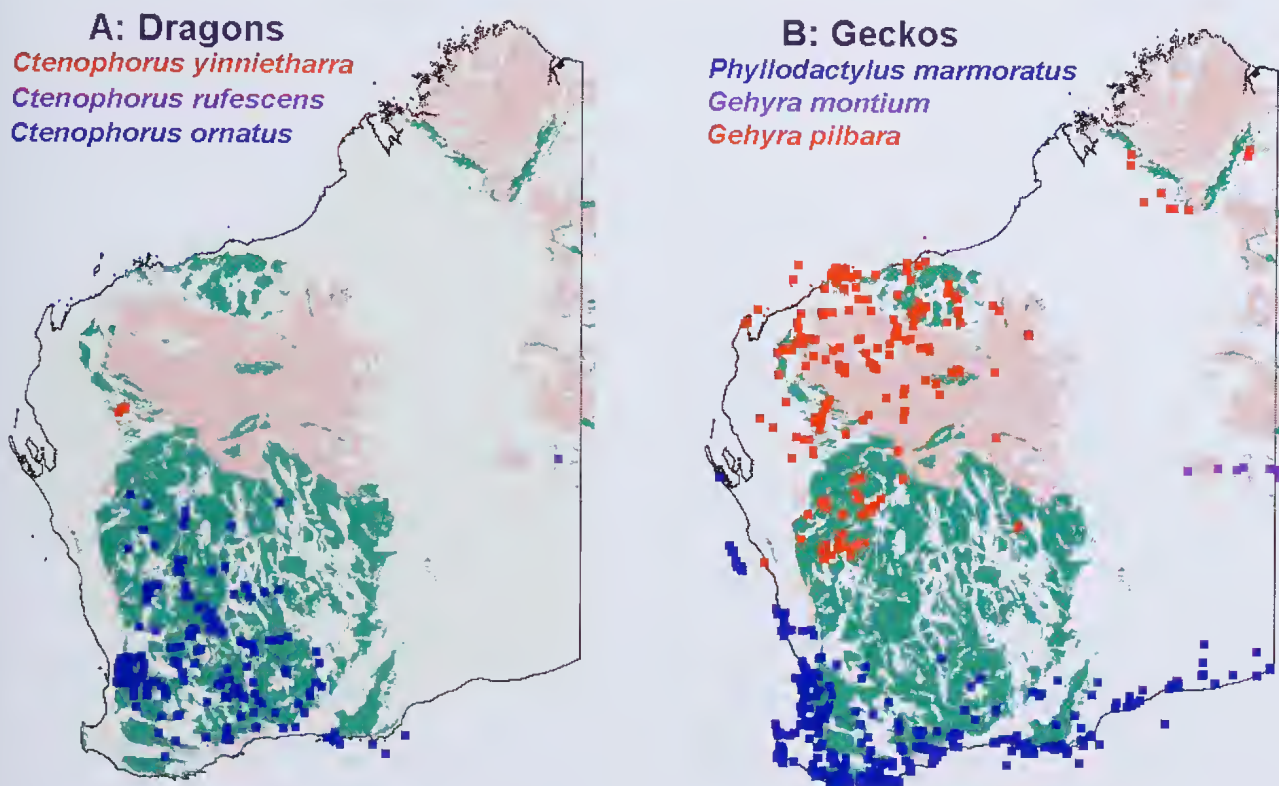


Figure 6. A: Distribution of *Ctenophorus ornatus* ($n = 802$ records), *C. yinnietharra* ($n = 19$) and *C. rufescens* ($n = 25$) with respect to granite landforms in Western Australia. B: Distribution of *Phyllodactylus marmoratus* ($n = 1337$), *Gehyra punctata* ($n = 696$) and *Gehyra montium* ($n = 83$) with respect to granite landforms in Western Australia. Distributional data from the Western Australian Museum; localities are plotted over the acid/intermediate intrusions (dark; corresponding roughly to granitoid in Fig 1) and proterozoic sediments (light; corresponding roughly to sandstone in Fig 1). AGSO bedrock data; graphed using Arcview by staff of the Western Australian Museum.

habitats is observed for the marbled gecko *Phyllodactylus* (*Christinus*) *marmoratus* (Fig 6B), with the coastal and island populations tending to use limestone and granite rocks more than trees. Similarly, the marbled velvet gecko (*Oedura marmorata*) is both arboreal and saxicolous.

In contrast to the relatively low number (4) of lizards restricted to granite rocks, a larger number (30) are restricted to sandstone rocks, or rocks in general (Table 1). Compared to one gecko restricted to granites, 9 species are restricted to sandstone or rocks in general. Compared to 3 dragons restricted to granites, only one additional species *C. caudicinctus* is restricted to rocks in general. Although no skinks were restricted to granites, about 10 species are restricted to other rocks. Finally, a number of goannas are restricted to rocky areas, particularly the sandstones of the Kimberley.

Birds

Birds, being generally more mobile than other terrestrial vertebrates, are less likely to be restricted to specific habitats, such as granite outcrops. Thus, although many species of bird have been recorded on granite outcrops (e.g. McKenzie *et al.* 1973; Dell & Johnstone 1976; Dell 1977; Youngson & McKenzie 1977; Hopper 1981; Dell *et al.* 1985), no species are restricted to them. In fact, the

dominant shrubs and mallees in the fringing apron around the rocks appear to be the main attractant to these birds, such as honey-eaters, and so granite rocks are exceptionally rich in honey-eater species compared with most wheatbelt habitats. Granite rocks represent one of the few habitat types that have not experienced extensive habitat destruction for agriculture and this increases their attractiveness to bird species (Hopper 1981). Water, when available in rock pools and gnammas, also attracts a number of bird species to granite outcrops.

Mammals

As with amphibians and birds, there are apparently no mammals restricted to granite outcrops, although a number of species are restricted to rocky areas. Rock wallabies (*Petrogale* spp) are an obvious example, being found in rocky habitats, including but certainly not exclusive to granite outcrops (Strahan 1983). The long-tailed dunnart (*Sminthopsis longicaudata*) is found in rugged, rocky areas of central Western Australia, and its long tail and striated foot pads apparently aid in rock climbing (Burbidge *et al.* 1983). Rock rats (*Zyzomys argurus*, *Z. woodwardi*) always are associated with rocky outcrops, particularly sandstones, of the Pilbara and

Kimberley. The rock ringtail possum (*Pseudocheirus dahli*) is found exclusively in rock outcrops of the Kimberley (Nelson & Kerle 1983).

Conclusions

Although granite outcrops occur over a large area of Western Australia, especially the western Yilgarn and Pilbara regions, very few species of terrestrial animals are apparently restricted to them. A few terrestrial arthropods, primarily *Teyl* spiders and the insect *Archaeochlus*, are known to be restricted to granites, which are presumably relictual habitats for these ancient genera. Some species of *Synsphyronus* pseudoscorpion and the embiopteran insect *Notoligotoma* may also be restricted to granite outcrops. Only four lizards are known to be restricted to granite outcrops, three dragons *Ctenophorus ornatus*, *C. yinnitharra* and *C. rufescens*, and the gecko *Gehyra montium*.

In contrast to the sparse list of species known to be restricted to granite outcrops, a very large number of terrestrial animals have been reported from granite outcrops. It is clear that granite outcrops are important as a seasonal resource for many animals or as a temporary refuge for the fauna of the surrounding habitats. In this regard, the fringing apron of modified habitat surrounding granite outcrops is an especially important aspect of the interaction between granite outcrops and their surrounding habitats, and must be preserved as vigorously as the granite outcrops themselves.

Acknowledgements: We thank numerous staff of the Western Australian Museum for their valuable discussions and generous sharing of data and ideas; R How, J Dell, L Smith, M Cowan, K Aplin, R Johnstone, M Harvey. We also are indebted to B York Main for sharing her wealth of knowledge on spiders.

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Invertebrates of temporary waters in gnammas on granite outcrops in Western Australia

I A E Bayly

Department of Biological Sciences,
Monash University, Clayton VIC 3168

Abstract

Thirty-six flooded gnammas (rock pools), distributed between 17 different granite outcrops, were each sampled once only during the winter of 1990. The water of most pools was acidic (pH < 7.0) and of low conductivity ($K_{25} < 200 \mu\text{S cm}^{-1}$). A total of 88 invertebrate taxa were found with *Boeckella opaqua* (Copepoda; 19 occurrences), *Cypretta baylyi* (Ostracoda; 17) and *Neotlirix armata* (Cladocera; 14) most common. A high proportion of the Crustacea consisted of species endemic to Western Australia. Six new species of *Cypricercus* (Ostracoda) were discovered. The mean number of taxa was 8.2 per pool. There was a highly significant positive correlation between species richness and the logarithm of both the pool volume and pool area. The nature of the fauna is reviewed within the framework of the type of adaptations employed by the animals for tolerating or avoiding the dry phase.

Introduction

The word "gnamma" is of Aboriginal origin and refers to a depression that has been weathered out of the surface of an outcrop of bare rock; some overseas workers (e.g. Smith 1941) have referred to these depressions as "weather pits". Gnammas, or weather pits, are commonly found on granite outcrops and especially on the top of domed inselbergs. Despite the widespread occurrence of gnammas in Australia, the aquatic biota of rain-filled gnammas has received remarkably little attention. This neglect might be partly explicable on the basis that, because gnammas are decidedly at the small end of the size spectrum of lentic waters (pool-pond-lake), they have been regarded as being of little interest or consequence to aquatic ecologists. In fact, small size confers on gnammas a number of methodological advantages, such as ease of sampling and experimental manipulation, as subjects for an ecologist. Sheldon (1984), for example, draws attention to the good potential of rock pools for comparative and experimental studies of the aerial colonization dynamics of adult aquatic insects. This claim for gnammas, along perhaps with phytotelmata (pockets of water held in plants such as the Albany Pitcher Plant; Bayly 1984), as being quintessential aquatic microcosms, is appealing. It may be claimed with some confidence, therefore, that the potential of studies of gnammas for illustrating ecological principles is just as great, if not greater, than that of large lakes.

Among the earliest written observations on the gnammas of Western Australian granite outcrops are those of the explorer Carnegie (1898). Interesting comments on the form, distribution and likely origin of granitic gnammas in this State were also recorded by the geologist Jutson (1934). Taxonomic work on invertebrates collected from Western Australian

gnammas has been undertaken by Wolf (1911), Fairbridge (1945), Petkovski (1973), Wallwork (1981), De Deckker (1981), Frey (1991, 1998), Lansbury (1995), Smirnov & Bayly (1995) and Benzie & Bayly (1996). Studies of the ecology of these gnammas, or of specific animals living in them, have been made by Jones (1971, 1974) and Bayly (1982).

Thus far only a limited attempt has been made to deal with the fauna of these peculiar and distinctive aquatic habitats in a comprehensive manner. The aim of this paper is to provide a fairly complete account of the invertebrate inhabitants of gnammas located in the more southern regions of Western Australia. This is a necessary basis for the future realisation of the above-mentioned potential of gnammas for facilitating ecological studies. Ecological aspects of the present study include the documentation of some salient chemical features of gnamma waters and the examination of species richness in relation to pool size.

This account is based on collections made from 36 gnammas, distributed between 17 different granite outcrops, during the winter of 1990. Thirteen of the 17 outcrops were in the form of domical inselbergs while the remainder were small flat surfaces. With one exception, the gnammas were shallow, flat-bottomed pan-gnammas *sensu* Twidale & Corbin (1963). The exception was a deep pit-gnamma located on War Rock.

Materials and Methods

The maximum depth, length and width (the greatest width at right angles to the line of maximum length) were measured at each pool. Hydrogen ion concentration and conductivity of water samples collected in a polyethylene bottle were determined with a Metrohm E588 pH-meter and Radiometer CDM2e conductivity meter respectively. Invertebrates were collected with a rectangular-framed net conforming with that described by Bayly (1982), except that the mesh

aperture was 150 μm , and preserved in either 10% formalin or 90% ethanol.

The product of the maximum length and maximum width of a pool was used to approximate (consistently overestimate) the true areas of the pools. Likewise, the product of the maximum length, maximum width and maximum depth was used to approximate (consistently overestimate) the true volumes of the pools. The approximated areas and volumes of the pools were log-transformed for correlation calculations.

Results

Data on the location and physical dimensions of the 36 pools as well as their water chemistry are presented in Table 1. With one exception, pH was within the range 4.6–7.9, but for 31 of the pools it was less than 7.0. With three exceptions, the conductivity (K_{25}) was less than 1000 $\mu\text{S cm}^{-1}$, and for the 33 pools whose conductivity was less than this value the mean was 147 $\mu\text{S cm}^{-1}$.

The results of taxonomic studies are summarized in Table 2. A total of 88 taxa were recorded and the mean number was 8.2 per gnamma. Branchiopod crustaceans were found in 18 pools, with *Limnadia* the most frequently occurring taxon. Cladocera occurred in 26 pools, with *Neothrix armata* the commonest species. Copepoda were found in 23 pools, with *Boeckella opaquia* occurring most frequently. Ostracods occurred in all but one gnamma and were the only animals collected from four gnammas. The commonest ostracod was *Cyprretta baylyi*. At least six new species of *Cypricercus* were recorded. Insects were found in 19 pools, with *Anisops thienemanni* the commonest species. Pools 16 and 21 yielded a disproportionately high number of insect species. Oribatid mites were restricted to two small coastal pools.

There is a highly significant, positive correlation between species richness and the logarithm of approximated pool volume (Fig 1; Pearson $r = 0.595$, $n = 36$, $P < 0.001$). If one outlier (two taxa from pool 19 with log volume 4.78) is removed from the data set, then the

Table 1
Physico-chemical features of Western Australian granite rock-pools sampled June–August 1990.

Locality number and name	Location (lat S, long E)	Sampling date	Maximum depth (cm)	Max. length x max. width (m^2)	pH	Conductivity (K_{25} ; $\mu\text{S cm}^{-1}$)
1. Coragina Rock (a)	32°55', 123°30'	24.vi.1990	25	16 x 7	8.7	91
2. Coragina Rock (b)	" "	"	6	3 x 2	6.4	59
3. Mt Madden (a)	33°14', 119°50'	26.vi.1990	30	30 x 10	6.3	74
4. Mt Madden (b)	" "	"	10	12 x 2.5	6.0	96
5. Mt Madden (c)	" "	"	15	5 x 2.5	6.1	38
6. Mt Madden (d)	" "	"	20	7 x 5	6.0	61
7. Cable Beach (a)	35°07', 117°54'	27.vi.1990	4	1 x 0.3	7.1	1480
8. Cable Beach (b)	" "	"	2	1 x 0.3	7.0	1490
9. Frenchman Bay Rd (a)	35°06', 117°57'	27.vi.1990	2	3 x 2	7.3	380
10. Frenchman Bay Rd (b)	" "	"	5	0.8 x 0.2	6.4	457
11. Muirillup Rock (a)	34°39', 116°15'	2.vii.1990	12	3 x 1.5	4.6	93
12. Muirillup Rock (b)	34°39', 116°15'	"	6	2 x 1.5	5.5	101
13. Cape Leeuwin (a)	34°22', 115°08'	6.vii.1990	2	2.5 x 1.2	6.7	450
14. Cape Leeuwin (b)	" "	"	4	5 x 1.5	6.5	8040
15. Bilya Rock	29°00', 115°51'	12.vii.1990	11	3 x 2.5	6.1	90
16. War Rock (a)	29°05', 116°00'	13.vii.1990	22	25 x 9	5.2	55
17. War Rock (b)	" "	"	>100	6 x 2	7.9	798
18. War Rock (c)	" "	"	12	4 x 2	6.1	38
19. Bunjil Rock (a)	29°39', 116°21'	13.vii.1990	100	10 x 6	6.8	60
20. Bunjil Rock (b)	" "	"	9	8 x 5	6.1	34
21. Petrudor Rocks (a)	30°25', 116°58'	14.viii.1990	80	11 x 11	6.5	116
22. Petrudor Rocks (b)	" "	"	6	3 x 1.5	6.0	186
23. Petrudor Rocks (c)	" "	"	19	6 x 3	6.2	190
24. Elachbutting (a)	30°36', 118°37'	15.viii.1990	10	6 x 2	5.1	164
25. Elachbutting (b)	" "	"	19	6 x 5	5.7	162
26. Sanford Rock (a)	31°14', 118°46'	15.viii.1990	26	8 x 3	6.3	102
27. Sanford Rock (b)	" "	"	12	2 x 2	6.7	88
28. Jilbadgie Rocks (a)	31°29', 119°13'	16.viii.1990	18	6 x 4	6.2	34
29. Jilbadgie Rocks (b)	" "	"	20	13 x 6	6.3	42
30. Mt Hampton (a)	31°45', 119°04'	16.viii.1990	33	10 x 9	6.3	144
31. Mt Hampton (b)	" "	"	13	4 x 3	6.4	64
32. Yorkrakine Rock (a)	31°26', 117°31'	26.viii.1990	9	7 x 5	6.4	113
33. Yorkrakine Rock (b)	" "	"	12	4 x 3	6.2	146
34. King Rocks (a)	32°19', 119°09'	28.viii.1990	20	14 x 10	6.6	105
35. King Rocks (b)	" "	"	30	16 x 8	6.4	91
36. Wave Rock	32°27', 118°54'	28.viii.1990	12	9 x 3	6.3	113

Table 2
List of taxa and their occurrences.

Taxa	Pool (see Table 1)	Total number of occurrences	Taxa	Pool (see Table 1)	Total number of occurrences
CRUSTACEA: ANOSTRACA					
<i>Branchinella longirostris</i> Wolf	5,24,25,26,27,31	6	<i>Cypricercus</i> sp or spp	6,20,22,26,33,34	6
<i>B. sp</i>	34	1	<i>C. n</i> sp 1	2,3	2
CRUSTACEA: CONCHOSTRACA					
<i>Cyzicus</i> sp	4,5,6,26	4	<i>C. n</i> sp 2	3,4,5,8,30	5
<i>Limnadia</i> sp or spp	15,22,25,27,28,29,30, 31,33,36	10	<i>C. n</i> sp 3	3,34	2
<i>Lynceus</i> sp	17,23	2	<i>C. n</i> sp 4	6,9,13,14,15,16	6
CRUSTACEA: CLADOCERA					
Chydoridae					
<i>Alona cf setuloides</i>	32,33	2	<i>C. n</i> sp 5	30	1
<i>A. n</i> sp	33	1	<i>C. n</i> sp 6	36	1
<i>Alonella - excisa</i> group	11	1	<i>Heterocypris incongruens</i> (Rahmdor)	2	1
<i>Biapertura - macropa</i> group			<i>Ilyodromus amplicolis</i> De Deckker	2,10,18,20,23,29,31,32,33	9
sp1	15	1	<i>I. candonites</i> De Deckker	9,12,16,18	4
sp2	11,35	2	<i>I. sp</i>	4,15,21,24,27,36	6
sp3	5,12,24,25,26,29,30,34,36	9	<i>Limnocythere mowbrayensis</i> Chapman	2,3,7,34,35,36	6
<i>B. rigidicaudis</i> Smirnov	6,27,28	3	<i>L. sp</i>	8	1
<i>B. n</i> sp	9,11	2	<i>L. n</i> sp?	13	1
<i>Ephemeroporus-barroisi</i> group			<i>L. n</i> sp	32	1
sp1	6,34,35	4	<i>Sarscypridopsis aculaeata</i> (Costa)	17,21,23	3
sp2	11	1	ACARI: ORIBATEI		
<i>Monospilus diporus</i> Smirnov & Timms	4,23,26	3	<i>Scapheremaeus</i> sp	78	2
<i>Planicirculus alticarinatus</i> Frey	26,31	2	<i>Trimalaconothrus</i> sp	78	2
<i>Plurispina chauliodus</i> Frey	12	1	INSECTA: COLEOPTERA		
<i>P. multituberculata</i> Frey	2,6,25,33	4	Dytiscidae		
<i>Rak stagnensis</i> Frey	1,4,5,27,29,34	6	<i>Allodessus bistrigatus</i> (Clark)	16,21,25	3
<i>Leberis aenigmatosa</i> Smirnov	27,29,31,34	4	<i>Eretes australis</i> (Erichson)	21	1
Other families					
<i>Daphnia jollyi</i> Petkovski	23,26,29,31	4	<i>Lanceles lanceolatus</i> (Clark)	6	1
<i>Neothrix armata</i> Gurney	13,6,12,15,18,21, 23,24,26,30,34,35,36	14	<i>Megaporus howitti</i> (Clark)	3,16	2
<i>Macrothrix breviseta</i> Smirnov	30,35	2	<i>Necterosoma darwini</i> (Babington)	11	1
<i>M. hardingi</i> Petkovski	24,27	2	<i>Paroster niger</i> Watts	78	2
<i>M. indistincta</i> Smirnov	1,25	2	<i>Sternopriscus multimaculatus</i> (Clark)	16,25	2
<i>M. longiseta</i> Smirnov	2	1	Hydrophilidae		
<i>Ceriodaphnia</i> sp	1,26,27,30,34,35,36	7	<i>Berosus approximatus</i> Fairmaire	16	1
<i>Moina</i> sp	1,2,15,18	4	<i>Limnoxenus zelandicus</i> (Broun)	6	1
CRUSTACEA: COPEPODA					
Calanoida					
<i>Boeckella opaquia</i> Fairbridge	1,2,3,4,5,6,24,25,26,27,28, 29,30,31,32,33,34,35,36	19	INSECTA: DIPTERA		
<i>B. triarticulata</i> (Thomson)	17,19,21,23	4	Ceratopogonidae		
<i>Calamoecia ampulla</i> (Searle)	21	1	<i>Dasyhelea</i> sp	2,22,25	3
Cyclopoida					
<i>Mesocyclops australiensis</i> (Sars)	21	1	Chironomidae		
<i>Metacyclops</i> sp	3,34	2	<i>Ablabesmyia</i> sp	28	1
<i>Microcyclops varicans</i> (Sars)	1,21	2	<i>Allostrissocladus</i> sp	28,30	2
Harpacticoida					
	11	1	<i>Chironomus tepperi</i> Skuse	2,23	2
CRUSTACEA: OSTRACODA					
<i>Alboia n</i> sp	16	1	<i>Dicrotendipes</i> sp	11	1
<i>Bennelongia barangaroo</i> De Deckker	1,5,23,25,29	5	<i>Paraborniola</i> sp	16	1
<i>B. sp</i>	3,21	2	<i>?Paratendipes</i> sp	33	1
<i>Candonocypris novaezelandiae</i> (Baird)	16	1	Orthocladinae	25,28,30	3
<i>Cyprretta baylyi</i> McKenzie	3,4,6,11,12,16,18,20,22,23, 25,26,27,28,32,33,36	17	INSECTA: HEMIPTERA		
<i>C. sp</i>	2,10,15,22,25,28,31, 32,33,34,35	11	Corixidae		
			<i>Agraptocorixa parvipunctata</i> (Hale)	3,6,16,21,23	5
			<i>Diaprepocoris personata</i> Hale	11	1
			<i>Micronecta annae</i> Kirkaldy	16,21	2
			<i>M. gracilis</i> Hale	21	1
			<i>M. robusta</i> Hale	4,6,25,26,36	5
			<i>Sigara mullaka</i> Lansbury	26	1
			Notonectidae		
			<i>Anisops baylyi</i> Lansbury	5,6,16	3
			<i>A. gratus</i> Hale	21	1
			<i>A. hyperion</i> Kirkaldy	3,6,17,21	4
			<i>A. stali</i> Kirkaldy	17,21	2
			<i>A. thienemanni</i> Lundblad	3,6,16,17,21,23,25,30	8

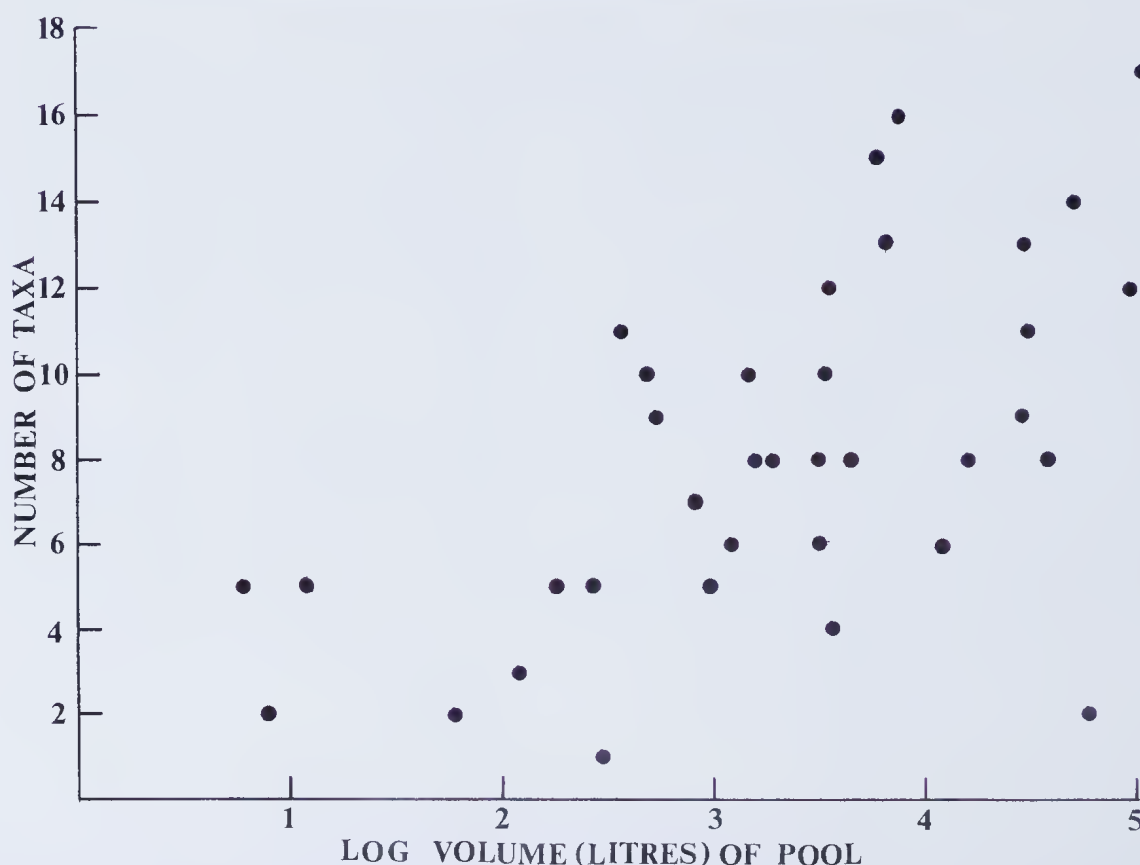


Figure 1. Plot of species richness against the logarithm (base 10) of the estimated volume (in litres) for all 36 gnammas. There is a highly significant positive correlation between these two variables (Pearson $r = 0.595$, $n = 36$, $P < 0.001$). The outlier at two species and log volume 4.78 is pool number 19 in Table 1.

correlation is considerably improved ($r = 0.696$, $n = 35$, $P < 0.001$). There is also a highly significant positive correlation between species richness (Pearson $r = 0.577$, $n = 36$, $P < 0.001$) and the logarithm of approximated pool area (Pearson $r = 0.641$, $n = 35$, $P < 0.001$).

Discussion

With seven exceptions, the conductivity (K_{25}) of the pools (Table 1) was less than $200 \mu\text{S cm}^{-1}$ – a finding broadly consistent with that of Bayly (1982) for a series of 19 granite rock pools in Western Australia. Six of the seven exceptions were pools with a maritime location (Cable Beach, Frenchman Bay and Cape Leeuwin) and whose high conductivities were clearly caused by the accession of ions from marine salt spray. The remaining exception was a deep pit-gnamma located on War Rock; this gnamma probably rarely loses accumulated ions by means of overflow.

The pH of almost all of the inland pools is acidic, as expected for a granite substratum. The exceptionally high pH recorded for Coragina Rock (a; Table 1) was discussed by Bayly (1992) who attributed it to the use of cement mortar between the exfoliated slabs of granite used to raise the level of the pool.

Although no quantitative data are available, it is noteworthy that granite rock-pools lack the high turbidity that is so characteristic of pools lying on the regolith, especially in arid regions.

The total number of taxa listed in Table 2 is 88. This, however, is an underestimate of the total number of metazoan invertebrate taxa because black planarians (*Bothriomesostoma*?) and nematodes were present in several collections but were not identified and are omitted from Table 2. The total of 88 taxa greatly exceeds the 18 invertebrate taxa listed by Bishop (1974) as occurring in a series of shallow pools located on sandstone at Kanangra Walls in the Blue Mountains, New South Wales. The 88 taxa from all 36 pools and the 17 taxa from the richest pool (number 21) may also be compared with the 121 invertebrate taxa reported by Lake *et al.* (1989) from a single temporary pond (not located on a granitic substratum) in western Victoria that was repeatedly sampled over 7 months.

The animals listed in Table 2 may be classified into four groups according to their adaptations for tolerating or avoiding the dry phase following the system of Wiggins *et al.* (1980) as modified by Williams (1985).

- **Group A** (Group I of Wiggins *et al.* 1980) consists of permanent residents of the pools that are capable of only passive dispersal. These organisms are dormant during the dry season and typically avoid desiccation as a resistant stage (shelled egg or embryo). All of the Crustacea listed in Table 2 should be assigned to this group, a salient feature of which is the high proportion of species endemic to Western Australia. Such endemics include *Branchinella longirostris*, *Daphnia jollyi*, *Macrothrix hardingi*, *Boeckella opaquia*, *Ilyodromus amplicolis*, *I. candonites*, *Leberis aenigmatica*, *Plurispina*

chauliodus and *P. multituberculata*. This list does not include the new species of *Cypricerus* some of which are likely to prove endemic. A distinctive negative feature of this group is the absence of notostracans. Despite their possession of a suite of adaptations (including resistant eggs) for occupancy of small temporary waters, an unknown factor excluded notostracans from granite rock pools studied here. A possible reason is that the concentration of calcium in waters on granite is so low that it is physiologically impossible for *Lepidurus* or *Triops* to fabricate their relatively large carapace. The carapaces of *Ilyodromus* and other ostracod taxa living in granite rock-pools contain practically no calcium; instead their carapaces are strengthened by non-calcareous ridges to compensate for this deficiency P De Deckker (*pers comm*).

- **Group B** (Group II of Wiggins *et al.* 1980) comprises animals (typically insects) that are capable of active dispersal but which are typically still present during the dry season in a dormant form (quiescent larvae). *Allotrissocladius*, *Paraborniola* and *Dasyhelea* are assigned to this group. The ability of the larvae of these taxa to resist desiccation in gnammas was investigated by Jones (1971, 1975).

- **Group C** (Group IV of Wiggins *et al.* 1980) consists of animals (typically insects) capable of active dispersal and which have a discontinuous presence in the pools; they avoid the dry period altogether by emigrating to permanent waters before the pools dry up. To this group are assigned all the Dytiscidae, Hydrophilidae, Corixidae and Notonectidae listed in Table 2, some 20 species in all.

- **Group D** [Williams' (1985) replacement for Group III of Wiggins *et al.*] comprises animals which lack a resistant stage in their life cycle but possess exceptionally good dispersal ability thus allowing a discontinuous presence in the confines of a temporary water basin. A single species, *Chironomus tepperi*, may be assigned to this group. The ability of this species to rapidly colonize temporary waters has been demonstrated by Maher & Carpenter (1984).

The biology of the oribatid mites, *Chudalupia meridionalis* (see Bayly 1992), *Scapheremnaeus* sp and *Trimalaconothrus* sp is insufficiently known to allow their assignment within the Wiggins-Williams system.

Wiggins *et al.* (1980) mentioned the habit of burrowing into bottom sediments as a behavioural adaptation for avoiding desiccation in temporary pools. While this pattern of behaviour may provide an escape for some animals in most pools, there is little scope for it in most pan-gnammas because of minimal amounts of sediment and the impossibility of burrowing into granite. Deep pit-gnammas left undisturbed for long periods may accumulate a significant amount of sediment and provide an exception.

Fryer (1985), on the basis of studies in England, concluded that chydorid cladocerans "show an unambiguous preference for large water bodies". However, this conclusion is of doubtful validity in the Australian context (Frey 1998). Although sampled once only, some gnammas contained four species of Chydoridae and there is presently no evidence that this number is significantly exceeded in large Australian

lakes. Timms (1981), for example, sampled the littoral region of Lake Purrumbete, a large (552 ha) freshwater lake in Western Victoria, monthly for a year, but recorded only six chydorid species.

The finding of a significant positive correlation between species richness and the volume of the pools is consistent with earlier investigations. Ranta (1982) reported a significant correlation between the number of water beetle species and the logarithm of pool volume in a series of 20 coastal (marine supralittoral) rock pools located in the Baltic region. A similar finding for a greater diversity of taxa was made by March & Bass (1995) for a series of six temporary pools located in Oklahoma.

Acknowledgements: I am very grateful to the following for providing taxonomic identifications; the late Professor D G Frey (Chydoridae), P De Deckker (Ostracoda), I Lansbury (Corixidae and Notonectidae), M C Geddes (Anostraca and Conchostraca), D W Morton (Cyclopoida), M Colloff (Oribatei), D H D Edward (Chironomidae and Ceratopogonidae), J F Lawrence (Hydrophilidae) and C H S Watts (Dytiscidae). Because of the importance of ostracods in gnammas, P De Deckker's task was a particularly onerous one. I thank the Royal Society of Western Australia for inviting me to contribute to the Symposium and for paying my travelling expenses. I am indebted to L Dembinski for the word processing.

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Aboriginal people and granite domes

P R Bindon

Department of Anthropology, W A Museum, Francis Street, Perth WA 6000
present address: 38 Mont Street, Yass NSW 2582

Abstract

Granite domes provided Aboriginal people living on the surrounding plains with a variety of economic products. Granite domes also acted as focal points for the activities of ancestral heroes who journeyed throughout the landscape. Aboriginal religious practice includes ritual dramas which replicate the activities of these ancestral heroes at such sites. Surface geology therefore determines both the economic practices and religious activities undertaken by Aboriginal people within their territories.

Introduction

Granite domes are prominent landscape features common to a large part of the southern central region of Western Australia, although they do occur in other places throughout the State. We can reasonably assume that granite domes have played important roles in the settlement and continued occupation of Western Australia since humans first arrived in the area, possibly some 125,000 years ago (Science, Oct 4, 274: 33-34; West Australian, Nov 16, 1996, 34). Not least in importance was the role that granite domes played in providing water in the arid interior, a function which continues to be crucial for many Western Australian towns (Simpson 1926). Use of waters collected on rock exposures allowed grazing in Western Australian shrublands which could not be reasonably exploited until subterranean water could be used (Dimer 1989). Much of the exploration of the State was accomplished by survey teams locating waters or persuading or coercing Aboriginal people to reveal water sources found on or adjacent to granite domes. For Aboriginal people, inselbergs provided or facilitated access to a wide range of resources other than water, but water was and remains crucial to human occupation of much of Western Australia.

Water Supplies

Physical composition and shape of granite domes determine their water-yielding capacity. Weathered surfaces with water-holding depressions of one shape or another are common to most granite exposures. One form of natural reservoir called a 'gnamma hole' contributes its Aboriginal name to Australian English. The common addition of the English 'hole' to this phrase is redundant as explained below. Gnammas are commonly found in granites, but these kinds of holes also form in lateritic and quartz arenite mesas.

Kavanagh (1984) limits his definition of gnammas to holes formed in granites and given the name 'gnamma'

by desert dwelling Aboriginal people. The word 'gnamma' originates further to the west than Kavanagh's usage suggests. According to Wilkes (1978:227) who compiled a dictionary of Australian colloquialisms, the first published usage of the term is by George Fletcher Moore. In his 'Descriptive Vocabulary' of Aboriginal words from the South-west of Western Australia, Moore (1842) lists 'amar' and 'gnamar' as meaning "hole or pool of water in a rock." Although we are not told which dialect this word is from, we can assume from other entries in Moore's lists that the word was applied in the south-west where Nyoongar people live and also perhaps a little further eastwards in the Goldfields (Bindon & Chadwick 1992).

Although the origin and development of gnammas is not known with absolute certainty, they are believed to be formed primarily by chemical weathering of less well consolidated portions of the rock (Campbell & Twidale 1995). Talbot, a geologist employed by the Western Australian Government in the early part of this century, separated gnammas into two types of holes capable of holding water (Talbot 1912). Elongated ones, which he thought probably developed along cracks and sheet joints formed his first group, and rounded ones, where globular feldspathic crystalline masses were eroded by carbonic acid produced by decomposition of vegetable matter trapped in an initial depression, made up his second group. Talbot believed that the activity of animals scratching for moisture as well as human excavation contributed to the development of gnammas. He based his conclusion on having observed soft decayed granite two centimetres thick lining a hole which he cleaned out at Day's Rock. This soft material could be removed from the surface with a shovel, but beneath this soft layer the rock was quite solid (Talbot 1912:39). We are given no estimation of how long it may have taken for this weakened material to form! The geologist Woodward thought gnammas formed through the rapid disintegration of certain coarsely crystalline pegmatite bunches in the granite, which had segregated out in the original processes of cooling of the molten mass. He says "...for it is in this class of rock [granites] that the "gnamma" holes occur, upon which in the past the aborigines [sic] and also many white explorers have had to rely for their water supply" (Woodward 1912:16).

Gnammas can vary in depth from a few centimetres

to 10 metres with a diameter up to two metres (Serventy 1973). Maintenance of these holes to maximise water retention and control quality was an important Aboriginal activity wherever the small reservoirs occurred. Mountford observed that "The Aborigines often cover these small but invaluable supplies, *nama*, with slabs of stone to minimise evaporation and prevent contamination by the creatures" (Mountford, 1976:42). Gnammas were considered important enough by European Australians to be marked on cadastral and geological maps until very recently.

During the Elder expedition through then unmapped south-eastern parts of the state, Helms made a number of observations concerning Aboriginal use of gnammas. He says "The rock-holes seem to be a special characteristic of this portion of Australia, and without them it would be impossible for the natives to exist. They are mostly found in granite, a softer mass or nodule having weathered away, thus forming natural cisterns of various shapes and dimensions. Some of them will hold many thousand gallons when filled, and as the water cannot escape by percolation the supply will last for a long time. To prevent animals getting at the water, most of the rock-holes are partly or entirely filled with loosely-lying sticks, which practice, necessary as it may be to save the water, deteriorates its quality considerably by making it often look quite black and giving it a fetid smell and taste" (Helms 1892:253).

Helms' observation was repeated or perhaps copied by the ethnographer Daisy Bates who says "Rock holes are found in granite hills, either at the foot of hills or on a slope, or even on the top of some of the hills. To prevent animals, birds etc., from getting at these holes, the natives sometimes fill them with sticks or branches, which not infrequently spoil the water, or give it a fetid taste, and smell" (Bates 1985: 263). Aboriginal people have indicated to me that the sticks allow animals to reach the water, drink and climb out of the hole without being stranded and dying by drowning. The sticks thus prevent contamination by animal carcasses.

Kavanagh examined water supplies in arid Australia from the perspective of their use in defence (Kavanagh 1984). His assessment of gnammas was that they are generally ephemeral, lasting for just a few months depending on the rate of evaporation and exploitation. He did not think that they were useful for defence purposes. His attitude demonstrates the difference between the understanding of arid land exploitation patterns held by desert dwellers and those of itinerant desert visitors. Aboriginal people generally first used ephemeral water resources which disappear most rapidly. Claypans and other playa lakes that have great surface areas and little depth diminish quickly through evaporation. Following observation of storms in particular areas, people moved to the recently watered area. There they exploited whatever food resources they could while awaiting game attracted by new growth, and the flowers and fruits that follow a month or more after the storm passes. During their wait, they used the water in the claypans for their daily needs. As these resources diminished, the group would move back to more reliable water sources, perhaps well-shaded deep rock pools in narrow rocky valleys. Being well acquainted with the probabilities of the climate

and knowing intimately all the water storages of their region, their actions and movement to new water sources were always carefully thought out with all likely possibilities considered. When the group did decide to move, their course would often involve travelling between a series of granite domes, which then became not only resource bases, but also navigational markers.

Daisy Bates emphasised the importance of knowing the exact location of these life-sustaining landscape features. The necessity for having great familiarity with the resources of the land was a lesson only learnt following great hardship by many European explorers of Australia. She said "What are called 'ngamma holes' are circular hollows in a sandstone formation found principally in the Eucla division, and east of the Coolgardie goldfields district. Every ngamma hole in his district is known to the native. Many of these holes contain hundreds of gallons of water, the quantity varying with the size of the hole" (Bates 1985: 264). Bates goes on to describe how water holes occur at certain intervals across the Great Australian Bight. These waters would have allowed Eyre to traverse this region much more comfortably if he, and his Aboriginal guides, had the knowledge of their location held by those who were familiar with the countryside.

A few European explorers who learned the hard way did not survive to pass on their wisdom (Maclaren 1912). Austin, who did survive, explored the State's Ashburton and Gascoyne regions and recognised the importance of gnammas. He recorded in his journal the following observations; [country] "...watered by holes in a granite rock, ... we depended on the precarious supply of rainwater accumulated in the hollows of the rocks, ... finding plenty of water here in the hollows of the rocks" (Austin 1856:236-239). His journey was possible because he and his party located these small water-holes. Until artesian sources were tapped, these uncertain resources provided the only surface water besides that flowing in the intermittent rivers following unpredictable rains. At one stage, Austin was warned by Aboriginal people not to enter the upper Murchison-Gascoyne districts except in the winter, because there was no water available except at that time.

Hunting and Gathering Sites

The run-off that provided surface water in gnammas, also permitted other forms of life to flourish on, but mainly around the base of, the inselbergs. This is not to deny the significance of the various plants and animals colonising the rock surface itself, but few of these were important for Aboriginal people except through the contribution they made to the life of the higher plants and larger animals usually hunted as game. Various plant species favoured the rim of rocky outcrops, exploiting the zone where run-off from the all too rare rainfall was concentrated. Two very important trees to arid land dwellers, Kurrajongs (*Brachychiton gregorii* F Muell) and Quandongs (*Santalum acuminatum* (R Br) D C) are commonly found around granite outcrops. They provide fruit, wood and sometimes medicinal products for Aboriginal people, but also attract emus and other bird-life. The

medicinally important Rock Isotome, (*Isotoma petraea* F Muell) and the Adjikoh or Warrain (*Dioscorea hastifolia* Endl in Lehm), a staple yam species, also favour granite outcrops. If for no other reason, Aboriginal people visited granite domes to exploit these resources. The occurrence of food plants and water also attracted animals such as macropods and reptiles, many of which also contributed to Aboriginal diet.

Austin observed "In many places about the country, and particularly near some of the rocks, brushwood fences are found that serve, or have served, the purpose of trapping game. These fences are about two feet high, and simply made of broken-down shrubs and branches of trees, mainly mulga, and converge to an angle after extending for a long distance over the ground" (Austin 1856:256). At the end of the fence or at the convergence of two of these, holes were dug into which fell any animals that followed the fences to a gap. In other cases nets were suspended to ensnare animals which traversed the fences to the narrowing funnel. Austin goes on to say, "Near the rocks I have seen them constructed in a zig-zag shape, with the self-acting trap at the apex of the angles furthest away from the rocks" (Austin 1856:256).

On a number of granite outcrops in the south-west, features called 'lizard traps' can be found. These take the form of a rock plate or slab up to about a metre in diameter that is propped up along one edge by a number of other rocks so that it lies at a slant. As there is no possibility of the top rock falling and holding the lizard, we can assume that these were not true traps. However, they may be purposefully built especially to encourage sustained lizard populations on selected rock exposures by providing protective habitats. One presumes that establishing environments like this ensured the visiting hunter of a supply of animals on recurrent visits. It has been observed that when disturbed away from cover on these rock exposures, and given an opportunity, lizards or any small game run directly to the dark shelter of these slanted rocks. Regrettably, there is no evidence from ethnography confirming the function of these rock structures. However, their existence provides more than a suggestion that an early form of animal husbandry may have been in operation on these granites.

During a trip by car between Perth and Albany, a now deceased Aboriginal man from the Great Southern region observed that the areas around some of the granite exposures we passed needed burning to 'clean them up'. He said that traditionally it was permissible to burn around granites quite regularly because the exposed rocks provided a refuge for animals living nearby that fled to the vegetation free area during the burn. He also observed that there was always a piece of adjoining bushland that did not burn because of the topography of the granites, so homeless animals could easily re-establish themselves. There is no easy way of verifying for how long such beliefs about the management of the environment surrounding granite domes have been held by Aboriginal people. Clearly, however, my passenger's understanding of the processes involved with managing the resources available in these environments was quite extensive.

Places Frequented by Heroic Ancestral Figures

Since all the members of any Aboriginal linguistic group claim to be a descendant of one or another of the ancestral beings, and since the people are living in the landscape created by these ancestors, it follows that every person is linked by their lineage to the landforms, to other living things in the same environment, and to the associated mythology. These various links dominate and to a great extent determine the actions of any individual. Mountford points out in relation to art "that, as the Aborigines' love for their country is so deep, and the myths that tell of its creation so strongly determine their lives and behaviour, these beliefs should be reflected in their art, about which little was known" (1976:55). Mountford's argument can be applied with equal weight to many other activities including songs, stories, ritual dramas and the like.

Having recognised that Aboriginal beliefs about the countryside are related to activities undertaken within that landscape by heroic ancestral figures, we can briefly examine the implications of these tenets. By re-enacting the activities of their ancestors during commemorative ceremonies, Aboriginal people re-affirm and reinforce their religious beliefs. Amongst the activities which ancestors first performed, and which modern Aboriginal groups often maintain, is the creative formative journey first taken by the ancestor figure during the establishment of the present landscape. These ancestral journeys began so long ago that they now possess the qualities of dreams. In affirming their veracity, Aboriginal people use mime, song and dance which bring the totemic ancestors to life before their human worshippers (Strehlow 1971:349). Thus, the activities of ancestral beings around granite domes which occurred during the *tjukurrpa* (Dreaming) are mirrored by the actions of the most recent Aboriginal groups.

Numbers of granite domes were used as ceremonial areas by Aboriginal people. This is partly due to the significance these places receive from being associated with ancestral figures, but there are many other reasons why particular sites were chosen as a focus of ceremonial activity. Stone arrangements often mark these ritual places. The constructions, formed from slabs and other weathering products from the inselbergs, take the form of a 'W', are erected as a sinuous line or may be piled into a series of scattered mounds. Although the particular ceremonies carried out at these places cannot be detailed, it can be assumed that these features represent aspects of landscape and are connected with initiation procedures. As a mark of respect to their Aboriginal custodians, such places should be avoided if they are encountered, and care should be taken that they are not disturbed. Their location should be reported to the appropriate authority (AAD, Western Australian Government, 1982).

Art Sites

Numbers of granite domes scattered around Western Australia and in other parts of the continent contain extensive galleries of Aboriginal art. The motifs may be recognisable but the themes are often arcane (Mountford 1976). Some regions, such as the Pilbara, have art that

seemingly has no relationship in motif or theme to any other Australian Aboriginal artistic province (Wright 1968). In this part of the state, painted art forms are comparatively rare. The various motifs are usually produced by hammering, battering or pecking away the dark patinated surface from the rock to expose the lighter coloured fresh inner core. The anthropomorphic figures produced by this method, are enigmatic in form, lyrical and dynamic in execution. They are evocative of an intense and complex motivation underlying their execution. Despite many years of study, their ultimate meaning remains elusive. However, it is possible that these human-like forms represent the larger-than-life capacities of ancestral heroes.

Just south of the Kimberley region, at the northern extent of the bloc of Aboriginal cultures belonging to the western desert, a very different art genre exists. Here, circular forms composed of a number of concentric rings are joined into larger compositions using one or more parallel straight or sinuous lines. These forms seem related to the well-known art style of central Australia that depicts features in the landscape as a series of concentric circles with paths between them depicted as lines. It is difficult to avoid the idea that these motifs sometimes represent or at least include the very location at which they are found, linking that place with other localities visited by some ancestor or another. Unlike the Pilbara art, which might represent the ancestors themselves, this art represents their journeys through the landscape. Such an interpretation was provided to me by a group of Aboriginal men who were explaining motifs painted on the waiting room walls at Wirrimanu airport (Balgo Hills).

It is not surprising that ancestral figures are believed to have visited the very localities that their modern heirs visit. The human aspect of ancestral behaviour means that these ancients too must hunt to eat, must drink, and in fact perform all the acts that are necessary for life. Dominating the otherwise level plains of much of inland Australia, granite domes not only form prominent navigational pointers and ritual centres, they also supply many of the daily needs of humans just as they are believed to have done for ancestral heroes.

Quarries

Very few portable Aboriginal stone artefacts have been found that are made of granite. The crystalline nature of this rock type makes it an unsuitable material from which to shape tools by flaking. However, some ground objects made from granite, including a few fist-sized pebbles used as hammers or millstones are in the archaeology collections of the Western Australian Museum. Large grinding plates of granite are also found, especially where seed-grinding contributed significantly to Aboriginal diet. Invariably, these granite grinding bases are made on an exfoliated plate-like piece of suitable size. Fissuring and thermoclastic weathering of the surface of granite batholiths results in the scalar detachment of successive layers of roughly circular rock plates that slide down the convex face and stack or heap as a talus at the foot of the slope. Aboriginal people most likely utilised these found

objects because there is no physical evidence on batholiths or on the grinding plates that they were detached from the parent body using artificial means. Around the base of granite domes, on the gently sloping aprons, areas used for seed grinding can often be seen. These consist of a polished or smoothed surface, about 40 x by 20 cm, with a central depression one or two centimetres deep. A variety of seeds collected on the surrounding plain from grasses, shrubs and trees was ground to flour or gruel in these depressions using a fist-sized millstone. There may well have been other uses of granite domes more ephemeral than this, but evidence is lacking for these.

Although structures interpreted as hunting hides or perhaps the walls of semi-permanent shelters can be found on the surfaces or in the surrounding scree slopes of granite domes in the north of Western Australia, these constructions cannot be considered as typical of Aboriginal activities on granite domes. Using loose tabular pieces from weathering processes, windbreaks can be made fairly quickly, particularly if some brushwood is incorporated into the structure. Lack of archaeological remains other than the walls in these structures hinders their exact interpretation, and the interpretations provided here reflect modern Aboriginal people's comments on the structures.

Temporal Perspectives on Aboriginal Use of Granite Domes

Aboriginal use of granite domes probably extends much farther back in time than archaeological investigations suggest. The concentration of resources available near these impressive landscape features was clearly of great importance to Aboriginal people, who may or may not have left physical evidence of their visits to the sites. As we have seen, one obvious indication of Aboriginal use is the occurrence of seed grinding bases that are specially common around the aprons of granite domes. Although certain mineralised depositions may be found in these grinding bases, there is still no satisfactory method for obtaining their age. Portable seed grinding bases made of granite slabs are sometimes found in dateable contexts within archaeological excavations, but their occurrence does little more than indicate that seed grinding is an ancient activity, and does not really elucidate usage of granite domes. Despite this general lack of information, some archaeological excavations have revealed a short chronology of Aboriginal people's interest in granite domes.

Walga Rock

The inselberg known as Walganna or Walga Rock, located about 60 km east of Cue, is some 1.5 km long and 500 m wide. It emerges from a very flat semi-arid landscape clothed with dispersed Mulga (*Acacia aneura*) woodland. Situated adjacent to a temporary water hole, a shallow west-facing shelter runs for more than a hundred metres on the south-west side. This shelter developed along sheet joints; the highest and deepest part evolving through haloclasticism as well as thermoclastically. The rear wall of the rock shelter is decorated with paintings in red, yellow and white pigments (Bindon *et al.*, unpublished).

A stratigraphic sequence established in the excavation of six square metres which reached about 3 metres in depth revealed three distinct sedimentary units. The upper unit is strongly evident of human activity and disturbed by numerous burrows. Two dates obtained from the lower part of this unit show that it covers the last millennium bp; Ly 2098 is $1\,040 \pm 180$ bp and Ly 2087 is 790 ± 160 bp. Below this, and in-filled between the lower series and the back wall of the shelter lies the middle unit. One date relates to a median layer of this complex; Ly 2099 is $3\,820 \pm 200$ bp. The lowest unit, the upper part of which trends toward the shelter, producing the internal segment of a complex cone of debris has two dates for a central zone; Ly 1847 is $9\,950 \pm 750$ bp and Ly 1846 is $7\,010 \pm 350$ bp.

Sediment analysis revealed that firstly a mass movement of sediments occurred, which, in conjunction with mobilised granitic sand, covered the flanking embayments and superficial slab of the batholith by around 10 000 bp. The summit of this depositional event is marked by a discrete zone of small thermoclastically produced platelets. This is evidence for a wet phase followed by a drier period. Between about 7 000 and 4 000 bp, a series of hydrological events took place that caused in-cutting and furrowing into the back portion of the sloping bank formed by the first deposits. Erosional unconformities confirmed that periods of climatic variation occurred, during which deposition and subsequent erosion of a number of separate sediments alternated. Around 3 820 bp, the deposition of the upper friable unit began. Its sub-horizontal arrangement, and feeble development indicate a marked decrease in detrital deposition and relative climatic homogeneity that continued to about 690 bp.

Evidence of human use of the shelter was found throughout the whole of the excavation sequence, giving us indications of human activity in the vicinity for the last 10 000 years. Occupation was intermittent and more or less in the same temporal pattern as delineated by other authors writing about arid inland Australia (Gould 1977; Smith 1988; Veth 1989). Periods of sparse use begin the sequence, followed by a gradual increase in visitation that culminates in an intensive occupation over the last few thousand years. At around 4 000 years ago, small delicately flaked stone tools begin to appear here just as they do around this time in many other Australian archaeological sites. A similar temporal sequence was discovered in another shelter in a granite dome close to the south coast.

Cheetup

Smith (1993) excavated a shelter, Cheetup, about five kilometres from the present shoreline in the Cape Le Grand National Park. This north-east facing shelter is situated on the top and northern end of a granite dome, with a commanding view over the surrounding plain. Protection is provided from cold winds and storms originating from the south and west. There is easy access to a mixture of vegetation zones that include heathlands dominated by the Proteaceae, thickets of Myrtaceae and several swamps. Excavations in the shelter revealed a complex but shallow stratigraphy about 60 cm in depth. Ten radiometric dates bracket various sedimentary events which extend beyond $13\,245 \pm 315$ bp (GX 6605).

Before this date, a pit was dug in the shelter floor. It was lined with *Xanthorrhoea* leaf bases and woody parts and filled with fruits of *Macrozamia reidlii* (Gaud) CA Gard. This particularly interesting discovery confirms ethno-historic descriptions of a food preparation technique made by early European settlers in the district. Toxins in *Macrozamia* fruits must be removed by leaching or fermenting and cooking before the fruits are rendered edible. Smith's (1993) discovery of this fermentation pit demonstrates that Aboriginal usage of this plant extends back almost 14 000 years into prehistoric times. Faunal and botanical remains recovered from the excavation point to a more or less stable ecosystem on the granite regardless of what occurred on the surrounding heathlands.

Recherche Archipelago

At the height of the last global glacial maximum around 18 000 bp, islands now forming the Recherche Archipelago were granite peaks in an extended coastal plain. This plain was some 60 km wide if we consider the coast to be located near the edge of the continental shelf at that time. Like mainland granite exposures, the islands have areas of shallow sands, soil and granite debris.

Dortch & Morse (1984) located ten open sites and 30 isolated artefacts on five of the Recherche Archipelago Islands. No shelters that could be occupied with comfort were found by them. During two visits to the Recherche Group, I also was unable to locate any shelters that showed evidence of extended human occupation. Seven of Dortch and Morse's sites are on Middle Island, one on Gulch Island, and two on Stanley Island. Basing their estimations on present-day water depths surrounding the islands, they considered that Middle Island was formed between about 11 000 and 9 000 years ago, with the smaller Stanley and Gulch Islands separating from the mainland 1 000 to 2 000 years later.

The ten island sites consist of scatters of between 14 and 99 stone artefacts. Apart from an infilled rockhole on Flinders Peak, Middle Island, from which 14 artefacts were retrieved, no stratified prehistoric archaeological features were discovered. Smith (1993) argued that the stone objects were discarded when the localities were the peaks of granite domes whose bases have subsequently been inundated. However, information about prehistoric aspect, vegetation association, access to resource zones, and distance to freshwater, are almost impossible to determine for these sites. Although most island sites are within 200 m of the present shoreline, this distribution pattern be partly a function of the elevation of the batholith above present sea levels and area of the exposure of the outcrop as well as factors relating to ground visibility. Obviously, with the coastline so distant for most of the time that the peaks seem to have been used, no suggestion is being made that these sites indicate some type of exploitation of the littoral.

Although there is not enough evidence to decide with any certainty what criteria were used by Aboriginal people to determine the location of these sites they offer evidence of a low intensity of usage during the time when the surrounding plains were occupied by Aboriginal hunters and gatherers. However, Smith (1993) argues that the sites on the islands represent a land use system that continued on post-transgressive mainland sites. She

bases this argument on the occurrence of scattered sites around granite domes on the mainland that contain the same kinds of stone artefacts as those found on the islands.

There is also some indication of Aboriginal presence on the islands during the post-contact period. Some assemblages contain Aboriginal artefacts made of European materials, for example china. These are assumed to be "linked with the presence of European and American sealers, who seem to have had with them Tasmanian women and other Aboriginal people" (Dortch & Morse 1984:34). One of the Stanley Island assemblages includes a tula adze of coastal chert. Tula adzes, hafted in the end of spearthrowers, continued in use until the mid twentieth century in areas to the north east of the study area, and along the coast towards South Australia. Local Aboriginal people claim to have visited these islands during the first half of the twentieth century specifically to exploit nesting birds, mainly mutton-birds and shearwaters that have rookeries on the islands. It is not unlikely that this adze may have been discarded either during the whaling and sealing period of the early nineteenth century or even more recently during raids on bird rookeries. The occurrence of Aboriginal objects manufactured from European materials indicates that, whether willingly or not, Aboriginal people continued their association with these off-shore sites. Following inundation of the surrounding plains, a hiatus imposed by lack of watercraft precluded access until relatively recently.

An Earlier Occupation?

Following the identification of tools manufactured from bones derived from extinct megafauna found in sediments cleared early this century from depressions in granite domes in the Balladonia district, I proposed in conjunction with several other authors based in the Western Australian Museum that Aboriginals had inhabited the region perhaps fifty thousand years ago (Western Australian Museum Palaeontology Dept registration numbers; 65.2.80, 79.11.1, 79.11.5, 79.11.6 and 79.11.10). This proposition was based on the presumed date of the final disappearance of certain species of megafauna. Bone tools are difficult objects for archaeologists to identify because the taphonomy of the archaeological material in a site is not always unequivocal. Lacking conclusive dating we have not pressed this claim. However, detractors have not been able to completely demolish our case. What our study did help to emphasise was the importance of granite domes to both Aboriginal people and European settlers in the region. The latter group enhanced the meagre supplies these natural depressions provided by removing calcretised infills with explosives to increase water holding capacity. While their activities produced the sample of fossil bone material, it destroyed all stratigraphic context.

Conclusions

Aboriginal people used granite domes and their surrounds for a wide variety of purposes. Material

evidence that dates the purely economic aspect of this exploitation system is lacking beyond about 15 000 years ago. Perhaps the most important use was in the realm of the ceremonial uses about which no detailed discussion is possible because of on-going ritual connotations. This situation has occasionally led to misunderstandings arising between Aboriginal people and those who wish to mine, quarry or cause other major disturbance to granite domes and their surrounds. When clear scientific evidence for use and value cannot be demonstrated, it is difficult to sustain arguments for non-disturbance. It is to be hoped that, dialogue can occur between the many groups within society who have interests in granite domes and their place in the landscape. With a broad understanding of community concerns, an understanding of the complexity of opinions about granite domes can be formulated and appropriate uses determined.

Acknowledgments: I thank M Smith, for permission to use unpublished material from her research on Esperance, R Chadwick, C Dortch and M Lofgren who commented on drafts of this paper. Opinions, errors and omissions are my own.

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Water harvesting from granite outcrops in Western Australia

I A F Laing¹ & E J Hauck²

¹Office of Water Regulation PO Box 6740, Hay Street, East Perth WA 6892

²Agriculture Western Australia 3 Baron-Hay Ct South Perth WA 6151

Abstract

The value of granite rock outcrops for water supply was noted by Lefroy in 1863, on his expedition to the area now known as the Goldfields. Since about 1890, public water supplies have been developed using runoff from rock catchments at approximately 200 locations throughout the Western Australian wheatbelt. Storage reservoirs are formed by concrete walls, reinforced concrete tanks or excavated earth tanks, which range from 500 kilolitres to 168 000 kilolitres. Runoff from rock outcrops is diverted to storage reservoirs using grouted rock or masonry walls on a slight gradient. Some measurements of runoff, and water storage and use characteristics are presented. Bores, wells and soaks have been developed in land adjacent to many granite outcrops. A review of the current situation gives the existing numbers of granite rock outcrops used for public water supply, along with the expected frequency and amount of use. The future role and value of rock catchments for wheatbelt water supply are described in the context of the Farm Water Plan.

Introduction

The unique hydrologic characteristics of inland south Western Australia result in a dearth of good quality surface runoff and groundwater. It is therefore not surprising that granite outcrops have been widely used for water supply development.

The value of granite outcrops as sources of water was recognised by early explorers. The Government, the Water Corporation, and the farming community currently use rock catchments for water supply and this use is likely to continue. However, some rock catchment water supply facilities may be surplus to current requirements, especially in the piped water scheme area, and a rationalisation process is being implemented as part of the Western Australia Farm Water Plan.

Early History

Erickson *et al.* (1973) refer to Lefroy, on his expedition in 1863 to the area now known as the Goldfields, having noted the value of the "bald hills" of granite for water supplies. A later example is given by Batchelor (1965) who described Holland's trek from Broomehill to Coolgardie in 1903. Holland dug a shallow well adjacent to a large granite rock on the east side of Lake Carmody, and obtained water from a gnamma at another site.

The discovery of gold at Coolgardie in 1892, and at Kalgoorlie in 1893 caused the population in Western Australia to increase from 49 782 in 1891, to 184 124 in 1901, and to 282 114 in 1911. The resultant increase in demand for water, grain and hay created an immediate need for water supplies for people and livestock. Davis (1977) reported that hundreds of shallow wells were constructed as public water supplies in many of the

remote Goldfields areas before 1900. Whittington (1988) quoted an 1894 Mines Department report showing illustrations of a gnamma hole and a shallow well associated with a granite outcrop. Whittington (1988) also described an excavated earth dam of 6 000 kilolitre capacity which was constructed before 1896 at Woolgangie, 130 kilometres east of Southern Cross. This Government dam collected runoff from a 60 ha rock catchment. The dam was 5 m deep. At that time, the daily demand for water by travellers and the railway construction contractor was 73 kilolitres. The Goldfields water supply scheme was constructed from 1896 to 1902.

Burvill (1979) reported that from 1905 the wheatbelt expanded into areas where springs and soaks of potable water occurred near granite rocks. Davis (1977) observed that hundreds of small excavated tanks were constructed in the cereal/sheep areas as agriculture began and developed. At least some of these supplies would have been adjacent to granite outcrops to take advantage of the regular runoff. Sutton (1925) described rock catchments as the best natural catchments for water harvesting, and included photos of a rock catchment in use on a farm at Koolberin, near Kulin.

Types of Water Supply

The simplest types of water supply associated with granite outcrops are gnammas, which are naturally-occurring reservoirs that collect runoff from the surrounding outcrop. Soaks and shallow wells are often located adjacent to granite outcrops where soil and rock formations are conducive to sub-surface water collection. Gnammas, soaks and shallow wells generally have a limited water yield and are therefore seldom used for public water supplies today. However, these sources of water were an important part of traditional Aboriginal culture.

Supplies with larger water yields are more likely to involve the construction of walls, weirs or tanks. Engineered water supplies consist of a storage reservoir

formed by constructing a concrete wall or weir in a rock valley, or by excavating an earth tank in clay subsoil adjacent to a granite outcrop. In such cases, runoff from the rock catchment is invariably collected using grouted stone or masonry walls surveyed on a slight gradient. A gradient of 1 in 200 was stated by Fernie (1930).

Collecting drains on the early structures were formed from slabs of exfoliated granite rock, which were roughly shaped and cement-grouted to form walls up to 0.6 metre high. There has been an increasing use of prefabricated concrete slabs for collecting-drain construction since about the mid-1960s.

Major Developments, 1921 to 1971

Fernie (1930) provided very detailed descriptions of water supply design and construction by the Government in the present central wheatbelt area. He referred in particular to supplies constructed during the 1920s at the following locations; Kondinin Rock, Egg Rock, Geelakin Rock, Karlgarin A, Glenelg Hills, Wilgoyne, Narembreen, Knungagin, Barbalin and Waddouring. A reservoir behaviour study was reported for a proposed reservoir at Gramphorne Rocks.

The Public Works Department (Anon 1946) described the No. 1 District Water Supply, which consisted of 600 kilometres of pipeline, three major rock catchment sources (Waddouring, Barbalin and Knungagin), which was designed to supply water to 200 000 ha of farmland, four towns, seven railway sidings and railway requirements at two locations, one on the Mt Marshall rail loop, the other on the Dowerin to Merredin rail loop. It also described the No. 2 and No. 3 District Water Supplies which each utilised rock catchment runoff. The No. 2 District Supply distributed water through 129 kilometres of pipeline to Narembreen, and to 48 000 hectares of farmland. The No. 3 District Supply distributed water through 74 kilometres of pipeline to Kondinin, and to 17 000 hectares of farmland. The water source information for the No. 1, No. 2 and No. 3 District Supplies are summarised in Table 1.

The Public Works Department (Anon 1946) also presented data relevant to water supply of some wheatbelt towns. Those with water supplies derived from rock catchments (1946 population in brackets) included Bruce Rock (600), Wagin (1200), Dangin and Quairading

(500). Fernie (1930) stated that drains, channels and intake works were designed on a rainfall intensity of 25 mm per ha. Although these rates were exceeded several times in a few years, the nature of the construction has ensured that no damage has occurred to structures and surrounding land.

The Public Works Department (Anon 1946) reported that following construction of the District Water Supplies in the 1920s, it was State Government policy to provide excavated earth tanks for public water supply. It was stated that 554 excavated tanks were constructed to provide for the horse traffic of the day. It was also stated that where possible, local small rock catchments were exploited to provide runoff to these excavated tanks, although it was also observed that these rock catchments were "relatively few".

Davis (1977) makes reference to public water supply construction that he was directly involved in at Dingo Rock and Hyden Rock in the period 1948 to 1951. He also referred to the following supplies which were constructed in the period 1963 to 1971; Mt Madden, Karlgarin B, Gramphorne, North Cleary, Dulyalbin and Roe Dam. Davis (1977) also referred to plans having been prepared for water supply construction on another nine granite rock outcrops. Lack of funding had delayed these projects, although one of those listed, Mt Hampton was constructed in 1994/95.

Value of Granite Outcrops as Sources of Water Supply

Measurements of runoff have been made from the 42 ha Puntapin Rock at Wagin, and from the 26.3 ha Hyden Rock at Hyden. The runoff measurements indicate an annual rainfall-runoff relationship of 45 to 47 per cent, although from individual storms, 80 per cent runoff may occur.

Fernie (1930) gave detailed design information for water yield from three classes of rock catchment. The design information was expressed as initial daily storm loss, and percentage runoff from additional daily rainfall. A daily rainfall threshold value of 1 to 5 mm is indicated by Fernie (1930), depending on rock surface character, steepness, the occurrence of rock breaks, total catchment area and time of year. Fernie (1930) stated that for daily rainfall greater than the threshold rainfall, between 60 and 90 per cent runoff could be expected, depending on the granite outcrop characteristics.

The general increase in water salinity in wheatbelt farmlands tends to increase the value of the water supplies developed from granite outcrops. The water salinity of rock runoff is less than 50 mg L⁻¹ total dissolved solids. Bettenay & Hingston (1963) reported that by far the best quality (less than 1500 mg NaCl L⁻¹) and most reliable sources of groundwater are to be found near the large granite bosses in the wheatbelt. Water supplies based on granite outcrops are very dependable and the amount of stored water does not vary from year to year as much as in farm dam water harvesting systems. Many farmers therefore value these supplies as sources from which to cart water. Granite rock runoff has very low turbidity, and is therefore quite suitable for pesticide spraying operations on farms. In those areas

Table 1

Water source information for the No. 1, No. 2 and No. 3 District Supplies.

WATER SOURCE	GRANITE OUTCROP CATCHMENT AREA (ha)	RESERVOIR STORAGE CAPACITY (kL)
Barbalin	110	168 000
Waddouring	35	36 000
Knungagin	65	100 000
Narembreen	48	69 000
Kondinin	28	43 000
TOTALS	286	416 000

where farm dam water is generally turbid, rock catchment runoff has additional value.

Current Utilisation of Rock Catchments

Several rock catchments are linked into the Water Corporation's piped water scheme, and the rock catchment runoff supplements the total scheme supply. The Water Corporation has estimated (Chamberlain, *pers. comm.*, 1996) that more than 625 Agricultural Area dams and tanks exist, and that approximately 200 of these directly utilise runoff from rock catchments. The more significant supplies with strategic value to the farming community are documented by Hauck *et al.* (1996). The water supply facilities at each site vary, along with the intensity of use.

Following development of a site as a water supply,

there is relatively little regular disturbance of the site by water users. In most instances, the water reservoir is located such that gravity inflow occurs from the catchment, and gravity outflow to a loading point (standpipe) occurs. This allows regular truck access to the standpipe to occur some distance from the rock outcrop, thus resulting in minimal environmental impact on the immediate surrounds of the granite outcrop.

Surveys of water carting practice have shown that many farmers within close proximity of rock catchment water supplies use these supplies on a regular basis rather than as emergency water sources. The Farm Water Plan is encouraging these farmers to reduce the amount of water carted, and to be more self-sufficient on their own properties. However, the need for a well-distributed network of emergency water sources will remain a vital part of Government response plans during times of severe water deficiency.

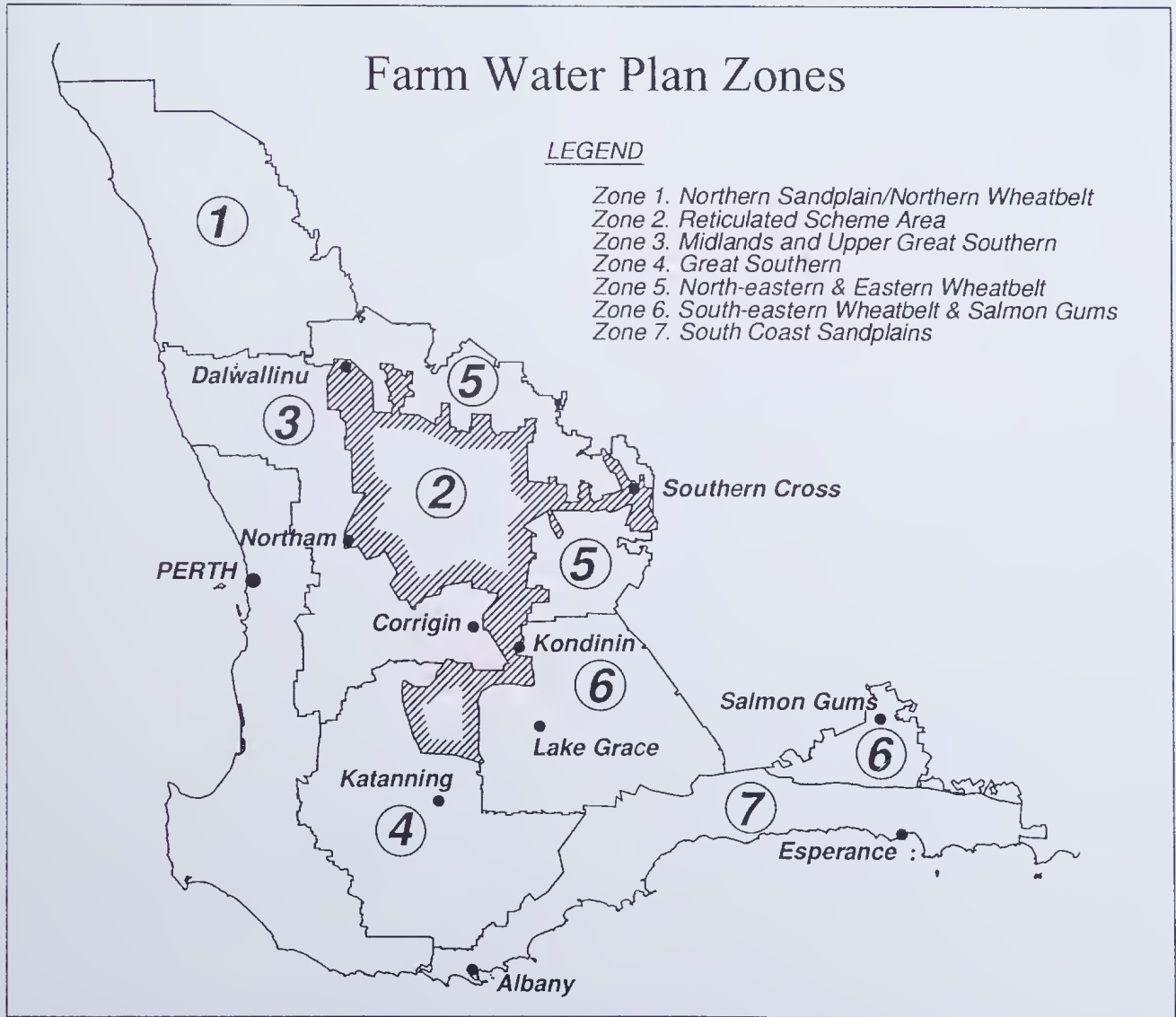


Figure 1. Map of Farm Water Plan Zones for south-western Western Australia (from the Office of Water Regulation).

Farm Water Plan

A Western Australian Farm Water Plan has been developed to cater for farm water supply shortages in dryland farming areas (Fig 1). The Farm Water Plan consists of six major integrated elements, one of which is the rationalisation of Agricultural Area dams and tanks (AA dams and tanks). These water supply facilities include the rock catchment water supplies. Many existing rock catchment water supplies are no longer needed for water supply purposes due to the surrounding farms now being served by a Water Corporation piped water scheme.

Government agencies are currently reviewing the network of AA dams and are identifying those dams and tanks for which there is an ongoing role. Disposal of surplus AA dams and tanks will be managed jointly by the Office of Water Regulation, the Water Corporation and the Water and Rivers Commission. Facilities to be disposed of will be offered to the Department of Conservation and Land Management, Local Governments, community groups or individual farmers. The disposal arrangements will, wherever possible, preserve any existing water supply value of the facilities. The network of AA dams and tanks in southern agricultural districts from Albany to Esperance is incomplete, and there is a clear need for more emergency farm water supplies to be provided in those areas.

The Office of Water Regulation is actively liaising with Local Government in these areas to establish permanent emergency farm water supply facilities.

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Management of granite rocks

A R Main

Department of Zoology, University of Western Australia, Nedlands WA 6907

Abstract

This paper discusses the possible goals of management of granite rocks in terms of the values associated with them and the sensitivity of different values to use. It is suggested that they may be viewed as rock islands. Many of the contrasting values are shared between the individual rocks and the surrounds *e.g.* picnic sites, but such contrasting habitats are not equally tolerant of disturbance. Problems associated with management are diverse and the task of managing rocks cannot be reduced to simple recipes. This paper sets out the difficult management problems which have to be resolved because of conflicts arising from the very disparate values attributed to rocks by different groups, and concludes that adequate management will depend on public cooperation based on an informed awareness of the diverse values attributed to rocks.

Introduction

Granite Rocks as a title would not pass with image makers or advertising copy writers who are skilled at attracting attention. As a term widely used to identify igneous (granite) or metamorphic (gneissic) rocks, to the public, the term evokes no special image except of mere rocks, usually with a rounded form which often stands above the surrounding countryside. Thus while the term is perfectly adequate as a descriptor it does not inspire any belief among the public that granite rocks have important attributes, especially any that would warrant efforts for their conservation or management. Management implies striving for a goal, to achieve something worthwhile, such as conservation. Such a suggestion leads to expressions of disbelief and the general response is to ask what is special or worthwhile about granite rocks? The pervasiveness of this attitude is manifest in the frequent laments about the paucity of information on the terrestrial animals of granite rocks. Clearly a team with a more evocative connotation would be helpful in stimulating interest and research. Other widely used terms are available, such as monadnock or inselberg. These have quite specific technical meanings as landforms but for conservation purposes where development of a conservation ethic and public support is required for success, a less forbidding term which will indicate to the public, the potential of rocks as sites for conservation, is needed. Island hills (Jutson 1934:350), the anglicised version of inselberg, suggests that the rocks, rising as they do from the surrounding countryside, may be viewed as the analogue of islands in the sea. Looked at in this way they may be seen as having potential as sites of biological evolution or be places where relicts of former plant and animal distributions may be found. Should this be so, then granite rocks have a significance in terms of the State's conservation strategy, one of its goals being to maintain biodiversity, as living resource conservation (Anon 1987). But, there are others in the community who are aware of other values possessed by

these rocky island hills. Because of these different values there is the potential for conflicts which lead to the need for a method of resolving them. A standard approach to such matters is to establish management goals and plans to achieve them. Whether such an approach is feasible for such isolated entities is the main test of this paper.

Management

Only a small proportion of the large number of granite rocks available are designated as, or are within, conservation reserves or State Forests. The Porongorups are a very large system of rocks and tors designated as National Park and therefore have a specific management plan. However, when included within larger reservations, granite outcrops are usually too small to be mapped at the scale commonly employed when devising management plans. Similarly, those granite outcrops within State Forests are not usually large; Christensen (1992:99) when writing of the karri forest makes the point under the heading of granitic monadnocks that "Many of the more prominent occur within parks and reserves; most of the remainder are in State Forests where they are secure because of their inaccessibility and absence of commercial value". Forest working plans may exclude granite areas from hazard reduction burns. Those occurring in the developed areas of the State are subject to a variety of uses and tenures; some are designated as water supply, others vested in local authorities, or are on private land or pastoral leases. They may be adjacent to or distant from settlement. A large number are unvested on vacant crown land. There is thus no hope of implementing a management regime run by a local or resident staff of rangers controlled by a central authority such as the Department of Conservation and Land Management. Moreover they are accessible. A more diffuse plan based on education, understanding of the problems and opportunities offered and involving co-operation between all those involved would seem to be a more sensible goal.

Ideally before management for conservation can be implemented it is necessary to know what is there, its rareness, abundance, whether it is replicated elsewhere

and its significance. Because flowering plants are easier to observe than animals their distribution and abundance is better known but in particular the question "Why and to whom are the features significant?" needs to be addressed because this will determine the nature of the conflicts which might arise when developing management plans. Also to be considered are the implications of this knowledge for historical interpretation as well as for management. Ultimately, the foregoing information will allow a statement to be made of what is to be managed, why it is to be managed *e.g.* significance in terms of uniqueness of landforms, rarity of biotic elements or their manifestation in an evolutionary or distributional pattern. Finally, it will be possible to assess how these attributes might be managed so that the elements of value for conservation are retained. Progress in achieving the above is possible once the basis of individual preference and perception of values can be established. But, granite rocks are usually so small and accessible that any management based on a system of zoning is impracticable.

Perceived Values

Values are established by people familiar with, and conscious of, the uses to which rock sites may be put. These include local residents, visitors, tourists and tour operators, botanists and zoologists, geologists (land forms, local water supply, quarry sites for road material and aggregate). In a general sense the usages can be classified as aesthetic and recreational (picnic sites, vantage points for viewing the countryside), cultural, (natural history *e.g.* displays of wildflowers in spring), heritage (historical sites, both Aboriginal and European) and utilitarian (quarry sites, water supply, slabs for facing culverts and channels for diverting run-off water into holding tanks, linings for wells in the apron soils adjacent to the rocks) and conservation. Additionally retention of aesthetic, recreational and conservation values is dependent on the maintenance of surrounding bushland from which lateritic gravel may be removed for road building material. Clearly these values are not all compatible.

Consequences of Use

Visitors, tourists and picnickers

This category of users do not see themselves as having much impact on the attractions of granite rocks. Nevertheless their compaction of soil at picnic sites at the rock base, initiation of erosion, trampling of lichens and displacement of slabs from rock surfaces lead to slow and irreversible degradation of the site. When such activities are accompanied by the use off-road vehicles which have an immense capacity to destroy the lichens of the rock surface, furrow the small rock bound meadows and disturb and pollute rock pools, the consequences are nothing short of catastrophic. Moreover, pristine rock pools frequently had slabs or rocks on their floor; when ponds dried these became sites beneath which frogs could over-summer (*Crinia*, *Pseudophryne*) or lay eggs before the pools filled in winter (*Pseudophryne*). Unfortunately, it seems to be common practice to gather rocks and slabs into piles or to throw them down rock slopes; either

activity destroys essential frog and lizard habitat and is the antithesis of good conservation practice. However, for those who enjoy the exhilaration of climbing to the top of the hill and viewing the country to the distant horizon these changes mean nothing.

Cultural

Wildflower displays in spring are the principal attraction. However, people are frequently attracted to mass displays of ephemerals such as everlastings (*Rhodanthe* and other composites) though some are especially attracted to orchids and other less conspicuous flowers. These flowering species vary in the intensity and size of their display depending on the season so most visitors understand the causes of the observed variability. Such is not the case with shrubs such as *Kunzea*, *Thryptomene* and other Myrtaceae which show a decline in vigour and failure to recruit. These changes are usually not remarked upon until the population approaches extinction. Even then awareness of the seriousness of the situation is only possible if the folk memory of the local population can recall what it was like in earlier times. Less conspicuous plants *e.g.* *Isoetes* or *Phylloglossum*, less spectacular flowering plants and invertebrates can disappear, without their loss being noticed, as a result of mere visitor pressure arising from activities mentioned in the previous paragraph.

Heritage

Few are aware of the significance of rocks as Aboriginal Heritage. Sites are known with stone arrangements and stenciled hands but the myths and legends relating to rocks and gnamma holes are little known. Information regarding the significance and distribution of localities needs to be assembled before appropriate management is possible. European heritage essentially begins with the early explorers who used, and were often dependent on, Aboriginal watering points. These water holes were essential for the maintenance of populations of birds and mammals. With the discovery of the Coolgardie and later the Kalgoorlie goldfields, heavily used trails were developed to them from York and Albany. These trails are characterised by the rocks, gnamma holes and watering points along the route. Later, many of these were used by early settlers and carefully constructed stone lined circular wells attest to their importance to both travellers and settlers. There is thus much of heritage value associated with rocks. Unfortunately it is easily destroyed and readily lost.

Utilitarian

Depending on mineral composition and rock fabric, granite rocks may be suitable as sites for quarries providing a source of aggregate for concrete making or road building material. Rock slabs resulting from exfoliation of rock surfaces were often cemented edge-on to form shallow spiral channels around rocks so that water normally shed to the apron soils was diverted into large holding tanks and thus provided a more dependable water supply. Such constructions destroyed much cover and many shelter sites for lizards which formerly frequented them. Furthermore, the diversion of water deprived the vegetation growing on the apron and surrounding soils of soil recharge with a consequent increase in aridity of these habitats.

Under natural conditions, water shed from rock surfaces contributed to ground water recharge, and much of this was subsequently transpired by the natural vegetation. However, in settled areas where natural vegetation is removed or reduced to mere fragments around rocks, transpiration is reduced and run-off from rock surface contributes significantly to ground water recharge and hence to rising saline water tables beneath soils of nature reserves and farms lower on the landscape. It is clearly an advantage to maintain native vegetation around granite rocks.

Conservation

The broad goals of conservation are to maintain biodiversity. This clearly has less tangible value than the matters discussed above. Maintenance of biodiversity can be seen as public good, the fulfilment of an ethical and moral obligation to cherish and leave an environment for the next generations that is as rich and enjoyable as the one experienced by the current generation. The values and usages enumerated in the preceding paragraphs are often incompatible with the goals of conservation. Moreover, it is often said that since conservation has no value in the market place, then it is not justifiable to use conservation value as an argument against useful developments. It is true that what nature provides as a free service is never appreciated in monetary terms until its loss has to be halted or the former service restored. In these terms one can look at the loss of picnic amenities, tourist dollars, or correction of rising saline ground waters as an approximation of the true monetary value of the so-called free services of nature. Management should address all of these issues while being aware that not only humans but feral animals such as cats, foxes and rabbits make a significant contribution to the loss of conservation values and biodiversity.

Discussion

Viewing granite rocks as islands suggests that the emergent rocks of the Western Australian plateau can be seen as an extensive archipelago stretching from the high rainfall South west to the arid interior. This interpretation offers special opportunities for management. In part this is because of the range of

climates spanned by their distribution, but recent geological history, when arid areas and their biotas expanded and contracted (Hopper 1979) has meant that many rocks in the region of fluctuating environment now have unusual combinations of biotic elements. Such rocks are of special significance as a record of the way the biota responded to past climatic changes. Additionally the array of rock islands offers an opportunity to establish the minimum viable population size of many taxa under an array of climatic and other conditions. This is an important practical and theoretical conservation problem so an opportunity to obtain an answer relevant to local conditions should be a major consideration for management.

The above discussion suggests that management will only be possible within a framework of social values, usage, cultural, geological and biogeographic history and conservation values. The complexity of the problems and conflicts along with possible management approaches are presented in Table 1. To the authoritarian mind, the complex set of interactions revealed in Table 1 can only be solved by having an enforceable set of rules accompanied by suitably punitive penalties. But such an approach implies a management presence which will be expensive. Equally it will tend to ignore special local circumstances and interests. Such an outcome leaves a disgruntled group who, more often than not, ignore the regulations. A more community centred programme based on discussions leading to the development of an understanding of the views and values held by others might be more rewarding.

Conclusion

Management of granite rocks will be complex and difficult. It will be impossible without a sympathetic and understanding public. Thus, before adequate management can develop, the public needs to become aware and appreciative of the values inherent in granite rocks. It is upon such an understanding that a satisfactory and enduring management can be developed based on a view of rocks as repositories of valuable information relating to Australia's biota as well as being venues for aesthetic, cultural, recreational and occasionally utilitarian values.

Table 1
Values, threats, conflicts and management of granite rocks

	Conservation	Recreation	Heritage	Utility
Values	All biota	Climbing, viewing, picnicking.	Aboriginal, Historical.	Watersupply aggregate, road material
Threats	Use, trampling, rock removal, picnic fires.	Overuse of picnic sites, soil erosion	Lack of awareness, failure to recognise.	Sites have other values
Conflicts	Recreational use is harmful	Use destroys other values	Other uses.	With all other values
Management	Education to appreciate values.	A caring responsible attitude.	Education, awareness	Regard for other values

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Geography, environment and flora of Mt Mulanje, Central Africa

J S Beard

6 Fraser Road, Applecross WA 6153

Abstract

Mt Mulanje in Malawi is the highest mountain in Central Africa, rising to 3002 m, and is one of the world's largest granite inselbergs. The mountain is formed of a series of coalescing domes of syenite, rising 2000 m above the surrounding plain. It is completely isolated and measures over 20 km at the base along each of its four sides. Almost bare slabs of rock sweep up from the base, covered with little but lichens and scattered *Xerophyta* plants. At about 1800 m, summits of some of the granite domes begin to provide plateau surfaces covered where the soil is deepest by the famous forests of Mulanje cedar *Widdringtonia nodiflora*, and where it is shallow and rocky by scrub. The latter community contains scattered individuals of a dwarf form of *Widdringtonia* with *Philippia benguelensis* and other species including *Protea nyasae* and *P. welwitschii*. Towards the mountain summits the composition of the scrub changes to dominance by *Erica whyteana* and *E. johnstoniana* with *Blaeria kiwuensis*. Lichens are dominant on exposed summits. The rainfall on Mulanje is said to be very high, between 2000 and 3000 mm annually, with a high incidence of cloud. The mountain is one of the most important surviving habitats for Afro-montane forest and fynbos scrub.

Introduction

Mt Mulanje is one of the world's most impressive granite inselbergs, a huge isolated mass of rock rising to 3002 m, which makes it the highest mountain in Central Africa. It is formed of a series of coalescing domes of syenite which stand up at least 2000 m above the surrounding plain. The mountain is completely isolated and covers an area of 640 km² (Eastwood 1988). When one visits Ayers Rock one is told that it is the "world's largest monolith", whatever that is supposed to mean, presumably an outcrop free from stratification, joints or fissures. Mulanje also fits that description and is many times larger than Ayers Rock in length, breadth and volume.

Geography and Geology

The mountain is situated at 16° S 36° E, well within the tropics. It owes its existence to the tectonic movements along the great African Rift Valley, in which it is situated some 200 km south of Lake Malawi (formerly Lake Nyassa) which lies in a particularly deep and well-marked section of the Rift. The lake, 600 km long, stands at 474 m above sea level and is 695 m deep at its deepest point. The lake is drained southward by the Shire River which flows to the Zambezi. The Rift Valley south of Lake Malawi contains a few smaller lakes, e.g. Lake Malombe and Lake Chilwa, but gradually ceases to have surface expression. The horst forming Mt Mulanje has been upthrust at the southern end of the Rift. Like the famous Mt Kinabalu (4100 m) in north Borneo, it is a mass of granite thrust upward by underground pressures and probably of no very great geological age.

Vegetation

Owing to its topographic elevation the mountain attracts a very high rainfall of between 2000 mm and 3000 mm annually, and is frequently covered by cloud. On the other hand, soils are generally shallow and patchy with much bare rock exposed and it is this factor, together with the fires that regularly sweep the mountain in the dry season, which principally determines the nature of the vegetation. Rock surfaces are never absolutely bare but are covered with lichens (*Peltula* and *Usnea* spp) and a sedge (*Coleochloa setifera*), forming grass-like tufts. Larger, woody plants grow in crevices. Where more soil is available these grow taller and more widespread, and eventually one particular shrub *Widdringtonia nodiflora* may assume tree stature and form extensive forests.

The botany of Mulanje was explored by Alexander Whyte in 1891, leading to the description of a number of new and endemic species. More detail is obtainable from the recent work of Chapman (1962), Chapman & White (1970) and Porembski (1996). When I visited the mountain some years ago, an expedition was kindly laid on for me by the Forests Department of Nyasaland, who provided four Africans as guides and carriers. The inaccessibility of Mulanje is such that it is one of the few parts of the world that have not been conquered, even now, by the 4WD vehicle, and we had to make the ascent on foot. The prospect at first was daunting. From gentle lower forested slopes the mountain suddenly sweeps up in towering slabs of bare rock covered only with lichens, *Coleochloa* and a few woody plants mainly *Xerophyta splendens* (Velloziaceae) growing in crevices. The *Xerophyta* community has many unusual features which have been described by Porembski (1996). Fortunately a path for the ascent was available, through less abrupt, bush-covered slopes. At about the 1800 m level we reached the top of the first ascent and gained an uneven plateau affording sweeping views of the clouds covering

the lower country around. From here too a view is available of the off-lying Chambe Peak of the main massif, embracing a plateau devoted to forestry where natural cedar forests are being worked and augmented by plantations. Timber is (or was at that time) extracted by aerial ropeway.

Eventually we reached the welcome shelter of the forest resthouse, Lichenya cottage, built entirely of local cedar timber with cedar shingles. The resthouse is surrounded by cedar forest formed by the cypress-like tree *Widdringtonia nodiflora* which is very similar to any Australian cypress pine (*Callitris*). Just as the latter usually represent a relict vegetation growing in fire-protected places, so *Widdringtonia* trees have evidently been more abundant in the past in more pluvial times. As with *Callitris*, e.g. *C. roei* in Western Australian kwongan, there has been a speciation into shrub-sized species which have become components of the South African fynbos. The trees on Mulanje are heavily lichenised as a result of the damp cloudy atmosphere. None-the-less, fires may often occur in dry periods in spite of the high rainfall, and the forest can be seen to be very patchy.

The summit of the mountain was in plain view from the resthouse, but having taken most of the day to walk up there, enough was enough for the present; I spent the evening in front of a cheerful log fire of cedar wood. Next morning, unfortunately and to my consternation, the clouds were down and we could see nothing. It was useless to try to find one's way to the summit under these conditions, so my African attendants and I padded around in the fog and the drizzle doing a little botanising. The following day was still cloudy but much better, and so it was decided to strike for the summit.

Shallow rocky places above the forest are covered by a scrub similar to the fynbos of the Cape mountains containing a dwarf form of the *Widdringtonia* with *Philippia benguelensis* and other species of Ericaceae, and an endemic protea, *P. nyasae*, which I was particularly looking for at the time. Higher up the composition of the scrub changes to dominance by *Erica* spp, chiefly *E. whyteana* and *E. johnstoniana*, with *Blaeria kivuensis*. These communities with local endemic species are typical of the so-called ericaceous zone of high East African mountains (Hedberg 1951). Some ericas are mat-forming species, while others are substantial shrubs.

Keeping the top of the mountain in sight, we luckily discovered a little track that had been beaconed, as I discovered later, by the Mountain Club of Nyasaland, and which led to the top. I was glad of this, as I was nervous that the clouds might come down again and make it difficult for us to find our way back. Luckily this did not happen, but one can understand that in a topography of granite domes to strike off straight down hill may lead one into a situation of even increasing steepness and can be dangerous. We returned safely and in clear weather. The summit has very little vegetation except lichens.

Biogeography

From the point of view of biogeography, the flora of East African mountains is interesting for its close

relationship to that of the Cape mountains in South Africa which are well known to feature a shrubland formation known locally as fynbos (Cowling 1992) in which woody species belonging to the families Ericaceae, Fabaceae and Proteaceae are dominant, with many herbaceous perennials in the ground layer, especially Restionaceae. Fynbos is in many ways similar to the kwongan of south-western Australia (Pate & Beard 1984), the principal difference floristically being that Ericaceae are replaced by Myrtaceae in Australia. As with kwongan, fynbos typifies a particular phytogeographic region known at one time as the Cape Floral Kingdom, nowadays preferably as the Cape Floristic Region. Climatically this is subject to a winter rainfall maximum in the west, merging into a non-seasonal regime in the east. Beyond the eastern end of the Cape Floristic Region the rainfall pattern changes to summer maximum which encourages the growth of grass, so that annual fires become a feature of the environment and grasslands are predominant. Within the fynbos region where grasses are insignificant fires occur less frequently and the shrubland can regenerate free from grass competition. In the summer rainfall area we have evidence from relictual patches that fynbos is properly the climax vegetation in the mountains but has been largely eliminated by burning (Beard 1993). Such relics continue to occur all along the mountain chains and escarpments of eastern Africa at increasing altitude right up to the Equator and beyond into Ethiopia.

Another feature of this situation is that small scattered populations of *Widdringtonia* are also found, the best known being in the Cedarberg in the western Cape mountains. These follow the fynbos relics as far north as Mulanje, beyond which they are replaced by *Juniperus procera* as the ecological equivalent. The fossil pollen record shows widespread abundance of *Widdringtonia* in the past and it is reasonable to assume that it represents a prior climax vegetation which preceded fynbos on poor acid soils in these mountain situations. *Widdringtonia* is very sensitive to fire and it can only have been dominant when fynbos fires were less frequent and destructive, perhaps when rainfall generally was much higher, and also when humans – particularly cattle-keeping humans – were less numerous. A parallel situation exists in Western Australia where small relict populations of *Callitris* exist in fire-protected places – on coastal islands which were not reached by aborigines, or on cliffs and rocky places in the interior where there is insufficient grass to carry fire (Beard 1990). In this context Mt Mulanje is the most important refuge for the survival of *Widdringtonia* populations.

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Inselberg vegetation and the biodiversity of granite outcrops

S Porembski, R Seine & W Barthlott

Botanisches Institut der Universität, Meckenheimer Allee 170, D-53115 Bonn, Germany
email: unb112@oni-bonn.de

Abstract

Granite inselbergs occur as mostly dome-shaped rock outcrops in all climatic and vegetational zones of the tropics. Consisting of Precambrian rocks, they form ancient and stable landscape elements. Due to harsh edaphic and microclimatic conditions, the vegetation of inselbergs differs markedly from those of the surroundings. Well defined inselberg habitats (e.g. cryptogamic crusts, rock pools, monocotyledonous mats, ephemeral flush vegetation) can be distinguished based on physiognomy. Plant diversity of inselbergs is influenced by both deterministic processes and stochastic environmental disturbances. The latter promote higher species richness due to the prevention of competitive exclusion. Considerable regional differences in floristic composition, life forms and species diversity exist concerning both the vegetation of whole inselbergs as well as those of individual habitats.

Introduction

Introduced by the German geologist Bornhardt (1900), the term "inselberg" has achieved general acceptance in international literature. As solitary, usually monolithic mountains or groups of mountains, they rise abruptly from the surrounding plains (Fig 1). Consisting of Precambrian granites and gneisses, inselbergs are old landscape elements that may possess an age of more than 50 million years. Bremer & Jennings (1978) and Thomas (1994) provide detailed surveys of their geomorphology. Inselbergs are widely distributed on the old crystalline shields and occur particularly in tropical and subtropical regions but can also be found in temperate zones (e.g. southeastern USA, southwestern Australia). Due to harsh edaphic (i.e. more or less devoid of soil cover) and microclimatic (i.e. high degree of insolation and evaporation rates) conditions, the vegetation of inselbergs differs markedly from that of the surroundings. In contrast to their temperate counterparts (for surveys of literature, see: Australia; Ornduff 1987; Hopper 1992; USA; Quartermann *et al.* 1993), tropical inselbergs have not yet attracted many biologists. In North America and Australia the interest in rock outcrop vegetation is well established and consequently there has been an impressive number of ecological studies, including reproductive ecology (e.g. Hopper 1981; Wyatt 1983), competition (e.g. Sharitz & McCormick 1973; Ware 1991) and speciation (Hopper & Burgman 1983; Moran & Hopper 1983). Apart from regional, rather descriptive studies for tropical inselbergs (e.g. Adjanohoun 1964; Bonardi 1966; Fleischmann *et al.* 1996; Granville 1978; Hamblen 1964; Ibisch *et al.* 1995; Porembski 1995; Porembski *et al.* 1994, 1996a; Reitsma *et al.* 1992; Richards 1957; Sarthou 1992; Villiers 1981), comparative analyses of their vegetation are rarely available.

Since 1991, the vegetation of African and South American inselbergs has been the focal point of research at the Botanical Institute, University of Bonn. Within the

frame of this project, primary emphasis has been both upon a comparative floristic analysis of tropical inselbergs and on the identification of ecological factors responsible for regulating the species richness of inselberg plant communities. The objective of the present paper is to provide a general overview of plant communities on tropical inselbergs in combination with some comments on the relation between regional floristic richness and species numbers on inselbergs.

Flora and Vegetation of Inselbergs

Floristically, inselbergs in different geographical regions are clearly distinct. Apart from families that are of certain importance in regard to species number on inselbergs throughout the tropics (e.g. Poaceae, Cyperaceae, Rubiaceae), there are also region-specific families. For details on temperate inselbergs see Ornduff (1987), Hopper (1992) and Quartermann *et al.* (1993).

- **African inselbergs:** Fabaceae, Scrophulariaceae and Lentibulariaceae belong to the most species-rich families. The percentage of endemics is comparatively low. Therophytes are the predominant life form. Floristic differences are low on a local scale (low β -diversity).

- **South American inselbergs:** Melastomataceae, Orchidaceae, Cactaceae and Bromeliaceae are the most species-rich and characteristic families. The percentage of endemics is high. Phanerophytes are the predominant life form, whereas therophytes are far less important. Local floristic differences vary greatly (high β -diversity).

- **Tropical Asian inselbergs:** These are particularly well represented on the Indian subcontinent (Krebs 1942). However, information about the floristic composition of their vegetation is very sparse (Bharucha & Ansari 1962; Willis 1906). From consideration of these works and of several local floras (e.g. Matthews 1991), it can be assumed that the vegetation of Indian and Ceylonese inselbergs is close to their African counterparts at the family and genus level.

The vegetation of granite outcrops harbours a high percentage of highly adapted functional plant groups.



Figure 1. Dome-shaped granite inselberg in Brazil (Minas Gerais, near Camponario).

Above all, poikilohydric vascular plants (*i.e.* "resurrection plants", providing many examples of convergently developed taxa) are exceptionally well represented. Additional quite typical plant groups are succulents (Barthlott & Porembski 1996) and carnivorous plants (Seine *et al.* 1995).

Inselbergs form isolated insular ecosystems that host a vegetation consisting of physiognomically defined and well delimited habitats. Most characteristic are cryptogamic crusts, seasonally water-filled rock pools, monocotyledonous mats, ephemeral flush vegetation and wet flush vegetation. In the following, short characteristics of these habitats are given. A more detailed description is in preparation.

Cryptogamic crusts

Exposed rock surfaces are almost completely covered by either specialized cyanobacterial lichens (typically *Peltula* spp) or cyanobacteria (frequently *Stigonema* spp and *Scytonema* spp; Budel *et al.* 1994), which are responsible for the characteristic brownish or greyish colour of inselbergs. In seasonally dry, savanna regions, cyanobacterial lichens dominate on granite outcrops, whereas under rain forest climates the rocky slopes are commonly covered by cyanobacteria. Particularly where seepage water is available, moss cushions (in West Africa,

frequently *Bryum arachnoideum*) may establish (Frahm & Porembski 1994).

Seasonally water-filled rock pools

These pools, water-filled after rainfall, soon dry out if not replenished by subsequent rain, and form temporal habitats. Short-lived herbs predominate. Besides species which are otherwise widespread on marshy ground (*e.g.* *Cyperus* spp, *Ludwigia* spp), there are specialists which are restricted to this habitat both on tropical and extra-tropical rock outcrops. Prominent examples are richly represented within the Scrophulariaceae, such as the Namibian *Chamaegigas intrepidus*, *Amphianthus pusillus* (southeastern USA) and species belonging to the genera *Lindernia* (*e.g.* *L. monroi* and *L. conferta*, Zimbabwe), *Dopatrium* (*e.g.* *D. longidens*, West Africa; Fig 2), *Glossostigma* (*e.g.* *G. drummondii*, Australia). Interestingly, there is a high percentage of poikilohydric species amongst these. Widespread on East African inselbergs are geophytic waterplants of the genus *Aponogeton* (*e.g.* *A. stuhlmannii*, Zimbabwe). Characteristic but frequently overlooked are geophytic *Isoetes* species (*e.g.* *I. nigrifolia*, West Africa) that have also been recorded from extra-tropical inselbergs, like *I. melanospora* (Georgia, USA) and *I. australis* (Australia). These terrestrial species can be considered to be Gondwanan elements which have only



Figure 2. The Scrophulariaceae *Dopatrium longidens* is a characteristic colonizer of seasonally water-filled rock pools on West African granite outcrops. Photograph by Nadja Biedinger.

little or no long-range dispersal ability (Taylor & Hickey 1992).

Monocotyledonous mats

Soil cover is usually absent. However, a substrate mainly consisting of decaying plant material is present. Carpet-like mats formed by Bromeliaceae, Cyperaceae and Velloziaceae cover even steep rocky slopes (Fig 3). In tropical Africa and Madagascar, Cyperaceae dominate (*Afrotrilepis* in West Africa; *Coleochloa* in East Africa and Madagascar) and Velloziaceae (Xerophyta) sometimes attain the status of co-dominants. On neotropical inselbergs, Bromeliaceae (e.g. *Pitcairnia* spp, *Dyckia* spp, *Vriesea* spp) and Velloziaceae dominate, whereas Cyperaceae (*Trilepis* spp) are of minor importance. On granite outcrops in southwestern Australia, several poikilohydric species of the genus *Borya* (e.g. *B. constricta*, *B. sphaerocephala*) form dense mat-like stands on exposed slopes. Mat-forming Cyperaceae and Velloziaceae possess convergently developed morphological (treelet-like habit), anatomical (roots possessing a velamen radicum; Porembski & Barthlott 1995), and physiological (poikilohydry) adaptations in order to withstand the harsh ecological conditions on inselbergs. Remarkably, most mat-forming species host a highly specific set of epiphytic orchids (e.g. *Polystachya microbambusa* on *Afrotrilepis pilosa* in West Africa).

Apart from monocotyledons, only a few other groups of vascular plants occur as mat formers on inselbergs, for example the poikilohydrous shrub *Myrothamnus* (*M. flabellifolia* in East Africa, *M. moschata* in Madagascar) and a number of likewise poikilohydric species of the fern genus *Selaginella* (e.g. *S. niamniamensis*, *S. dregii* in East Africa; *S. convoluta*, *S. sellowii* in Brazil).

Ephemeral flush vegetation

This term was introduced by Richards (1957) and denotes a vegetation type developing at the base of steep slopes over thin soil where water continuously seeps during the rainy season. Poaceae and Cyperaceae make up the largest part of the phytomass. Most striking are tiny ephemerals with members of Eriocaulaceae, Xyridaceae, Burmanniaceae and carnivorous plants (Fig 4; Droseraceae and Lentibulariaceae; *Utricularia*, *Genlisea*; Seine *et al.* 1995). In tropical Africa, this community is especially well developed (*i.e.* most rich in species) on inselbergs situated in savanna zones (Dörrstock *et al.* 1996).

Wet flush vegetation

This occurs on inclined, bare rocky slopes where water flows continuously during the rainy season. Typical are small-sized annuals, in particular *Xyris* spp and *Utricularia* spp, which are attached to cyanobacterial



Figure 3. Mat-forming monocotyledons (here a bromeliad *Encholirium* sp) are a typical element of the vegetation of tropical inselbergs. Photograph by Nadja Biedinger.

crusts. Occasionally, small patches of mosses can be found which provide establishment sites for other vascular plants. This community develops best under humid tropical climates.

Despite fundamental floristic differences, the physiognomy of plant communities on inselbergs remains largely unchanged throughout the tropics. Inselbergs located in temperate regions are very similar to their tropical counterparts in regard to habitat composition. However, a major difference is evident in the widespread occurrence of monocotyledonous mats on tropical outcrops and their near absence from temperate inselbergs. The reason for this distinction is not clear yet. Presumably, climatic conditions (*i.e.* low temperatures) are responsible for the absence of slightly succulent (*e.g.* Bromeliaceae) or poikilohydric monocotyledons.

Species Diversity of Plant Communities on Inselbergs

Traditionally over the past, islands have played a crucial role in ecological studies designed to achieve a better understanding of those factors influencing the species richness of habitat fragments. Though the bulk of

scientific interest was directed to oceanic islands, naturally occurring continental island biotas may provide even better opportunities (*e.g.* because of less anthropogenic interference) for such studies. Due to their worldwide distribution, granitic outcrops offer excellent venues for comparative phytogeographical studies as well as for research on the controlling factors of species richness in isolated plant communities. Within the frame of this paper, consequences of abiotic influences and implications of biotic interactions for the diversity of the vegetation of inselbergs will be examined (for more details see Porembski *et al.* 1995, Porembski *et al.* 1996b).

Seasonality promotes higher species diversity

Observations on inselbergs in the Ivory Coast have revealed considerable habitat-specific differences in both alpha (*i.e.* the number of species) and β -diversity (*i.e.* the degree of change in species diversity along a transect or between habitats; Magurran 1988) between *Afrotrilepis* mats extending over large areas of rock and ephemeral flush communities which usually cover only a few square meters. In contrast to the almost monospecific monocot mats, which are dominated by the highly competitive Cyperaceae *Afrotrilepis pilosa* (with stems more than 1 m high, attaining an age of several hundred years), ephemeral flush communities may harbour several



Figure 4. Tiny annuals and carnivorous species (*Drosera indica*) are the characteristic components of ephemeral flush communities on tropical inselbergs (Benin, West Africa). Photograph by Nadja Biedinger.

dozens of tiny ephemerals. Each year, with the onset of the first rains in the rainy season, the component species of the latter community must establish themselves anew, leaving much room for stochastic events. It is this abiotically driven dynamic between dry and rainy season that may prevent competitive exclusion, and therefore guarantees the persistence of a highly diverse plant community. The bulk of ephemeral flush species is very small (*i.e.* less than 15 cm in height), and most species are generally considered as weak competitors (*e.g.* the carnivorous plants). In contrast, the species-poor *Afrotrilepis* mats are in a state of equilibrium with *Afrotrilepis pilosa* which is the clearly dominating element, leaving few opportunities for the establishment of additional less competitive species.

Species diversity not only varies between different inselberg habitats, but there is also a considerable degree of within-habitat variation in species diversity along ecological gradients. For most habitats on Ivorian inselbergs, a decline in species diversity along a gradient from the seasonally dry savanna region towards the rainforest zone was observed that is in marked contrast with the diversity of the surrounding vegetation. Again, it is possible to conclude that climatic seasonality favors the maintenance of species-rich plant communities on inselbergs by preventing competitive exclusion. The

declining diversity of inselberg vegetation in the Ivory Coast from savanna towards rainforest is probably enforced by increasing isolation of rock outcrops in the latter region. Granite outcrops are less frequent in the rainforest zone which, also lacks further azonal habitats such as ferricretes. In the savanna zone, the higher number of inselbergs and ecologically similar sites may serve to reduce extinction rates (via metapopulation dynamics) and thus promotes more species-rich communities.

Regional differences in plant species-richness on inselbergs

Studies on inselberg vegetation in different parts of the tropics showed large regional variations, both floristically and in regard to plant species-richness. The exact reasons for the pronounced differences in local plant species diversity on inselbergs situated, for example, in the Upper Guinea region of West Africa (low diversity) and in the Brazilian Atlantic rainforest (high diversity) have not been analyzed in detail yet. However, we assume that this difference is a consequence of the higher regional species diversity of the latter region (one of the global centers of biodiversity), resulting in a greater number of potential colonizers of inselberg habitats. This is illustrated by the considerably higher number of mat-

forming species on Brazilian inselbergs (more than a dozen species of Bromeliaceae, Velloziaceae, Cyperaceae; unpublished data) compared to the more or less monospecific *Afrotrilepis* mats on West African inselbergs. On the local scale the species richness of the vegetation of inselbergs is probably also influenced by processes, such as source-sink effects and metapopulation dynamics which both affect extinction rates on rock outcrops (Porembski *et al.* 1996a).

It has to be the aim of future comparative studies to explain existing floristic differentiations and the variations in plant species diversity between inselbergs located in geographically distinct areas. Because they are relatively uniform in geology, granitic and gneissic inselbergs offer a unique opportunity for the search for general determinants of species diversity in plant communities.

Acknowledgements: Financial support by the Deutsche Forschungsgemeinschaft (DFG-SPP "Mechanismen der Aufrechterhaltung tropischer Diversität") is gratefully acknowledged. The authors would also like to thank our Australian colleagues and, in particular, SD Hopper (Perth, Kings Park and Botanic Gardens) for support during fieldwork in Australia.

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Remnant vegetation, priority flora and weed invasions at Yilliminning Rock, Narrogin, Western Australia

J P Pigott & L W Sage

Department of Conservation and Land Management, Science and Information Division, WA Herbarium,
Locked Bag 104, Bentley Delivery Centre WA 6983
email: patrickp@calm.wa.gov.au

Abstract

Remnant vegetation on and around Yilliminning Rock, a granite inselberg near Narrogin, Western Australia, was surveyed several times between 1992 and 1997. Six plant communities comprising 238 vascular species from 54 families are reported. These include 2 undescribed species and 5 priority species; many of these populations are reported for the first time. In addition to the diverse vascular flora, 33 species of lichens from 11 families, including 2 priority species, are recorded for Yilliminning Rock. Of 19 recorded introduced vascular species, several are serious environmental weeds. The weed threat to populations of priority species and other management issues of concern are discussed.

Introduction

Yilliminning Rock is located in the Shire of Narrogin, about 230 km south-east of Perth, on the western edge of the Western Australian wheatbelt (Fig 1). The rock is a granite inselberg, rising to approximately 48 m, with commanding views across the farmland and remnant vegetation of the surrounding agroecosystem. Yilliminning Rock is a prominent feature in an undulating transitional landscape; less dissected and with fewer large granite outcrops than the Pingelly district to the north (Beard 1980). This contrasts the flat landscape to the southeast that includes the extensive wetlands of the Northern Arthur River System.

Beard (1980) describes the vegetation type around Yilliminning Rock as York gum (*Eucalyptus loxophleba*) and wandoo (*E. wandoo*) woodlands with some heath vegetation dominated by *Dryandra* species. However, this is more typified by remnant vegetation at Birdwhistle Rock about 20 km to the north-east. Here there is also rock sheoak (*Allocasuarina huegeliana*) forest, but with less prominent granite outcropping and a more visible disturbance history (e.g. stock grazing) and weed invasion than is apparent at the Yilliminning Rock reserve. The remnant woodlands and heaths around Yilliminning Rock have more in common with the vegetation types described for the Dryandra Forest to the northwest (see Coates 1993), although there are no large granite outcrops there. In fact, most of the granite outcrops mapped in the area by Beard (1980) have been cleared, with the exception of a small remnant about 10 km to the south near Nomans Lake (unpublished observations).

Yilliminning Rock occurs on a reserve of 86 ha, vested in the Shire of Narrogin as an A Class Reserve (11016) in 1960. The reserve was originally set aside for water and recreation in 1906, when the area was first surveyed for

agriculture. Yilliminning Rock is surrounded by about 60 ha of remnant heath and woodlands to the north and west and bordered by farmland on its east side (Fig 2). The Harrismith Road, which runs along the southern edge of the rock, provides access for the steady number of visitors from the town of Narrogin, 17.5 km to the west. Spectacular views in all directions are found at the top of Yilliminning Rock, which takes about 10 minutes to climb. With abundant wildflowers in winter and spring, the bushland at the base of the rock provides an attractive setting for picnics and walks.

This paper primarily describes the vegetation and flora of Yilliminning Rock and adjacent remnant vegetation. Secondly, it discusses the current threats to the nature conservation values of the remnant vegetation, as a basis for future management.

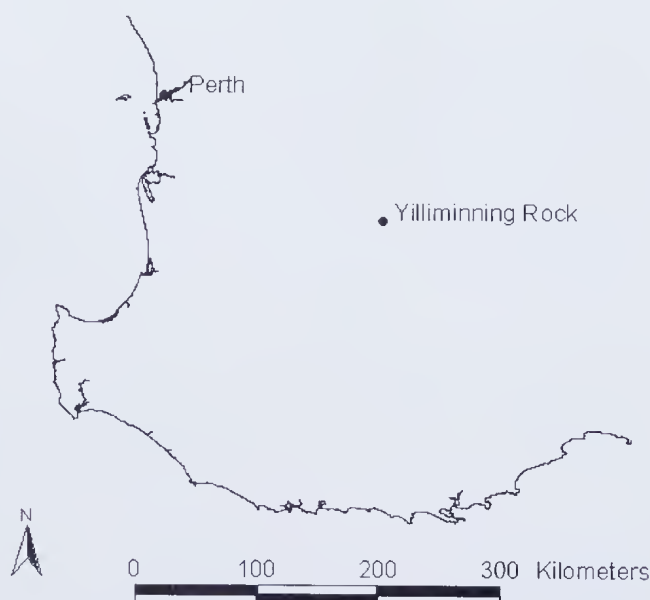


Figure 1. Location of Yilliminning Rock near Narrogin in the south-west of Western Australia.

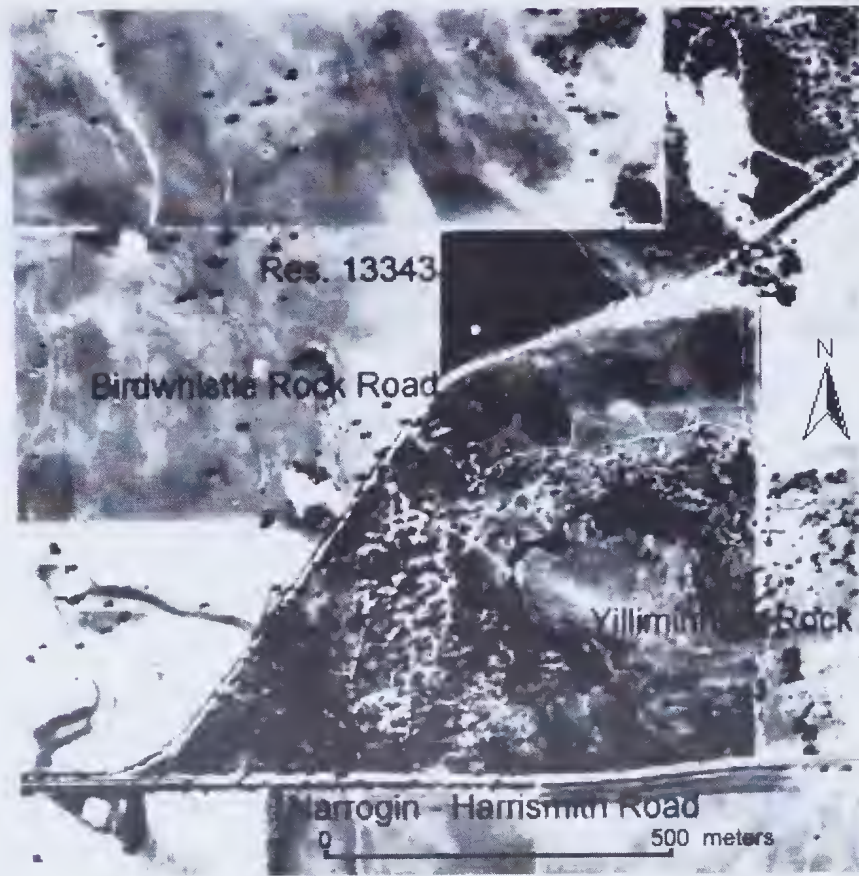


Figure 2. Aerial photograph of Yilliminning Rock Reserve, near Narrogin, Western Australia.

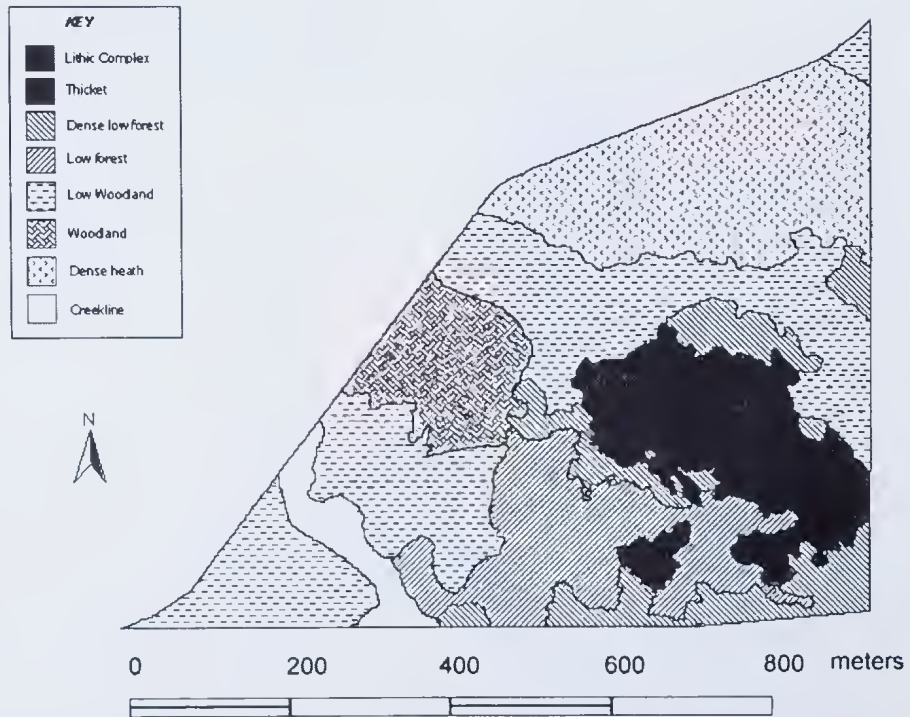


Figure 3. Vegetation map for Yilliminning Rock Reserve with vegetation associations from Table 1 shaded as Lithic Complex (1), Thicket (2), Dense Low Forest (3a), Low Forest (3b), Low Woodland (4), Woodland (5) and Dense Heath (6). The creekline running across the southwest of the reserve is unshaded.

Materials and Methods

Vegetation at Yilliminning Rock was mapped from a 1972 aerial photograph (Fig. 2) and 1996 remotely sensed image data (*unpublished data*). Associations and ecotone boundaries were checked during field surveys in 1996 and 1997. A list of species for Yilliminning Rock was compiled from records of the WA Herbarium (WAHERB) and collections made in spring 1992 (Anon 1993) and 1996 and autumn 1997. The survey technique known as 'randomized stratified walk' (Hopper *et al.* 1997) was used to sample each of the observable vegetation associations. This included a detailed circumnavigation of apron vegetation around Yilliminning Rock and several systematic traverses over the top of the rock.

Vegetation classification of associations follows Muir (1977). The authors identified specimens with assistance from staff of the WA Herbarium and S Hopper, Director of the Kings Park and Botanic Gardens. Nomenclature follows WACENSUS (WA Herbarium census of Western Australian vascular plants) and conservation status of species assigned from Atkins (1996) according to the following definitions (Table 1).

Table 1

Categories of Priority Flora according to the degree of perceived threat.

Category	Definition
Priority One – Poorly Known Taxa	Taxa which are known from one or a few (generally <5) populations which are under threat.
Priority Two – Poorly Known Taxa	Taxa which are known from one or a few (generally <5) populations, at least some of which are not believed to be under immediate threat <i>i.e.</i> not currently endangered.
Priority Three – Poorly Known Taxa	Taxa which are known from several populations, at least some of which are not believed to be under immediate threat <i>i.e.</i> not currently endangered.
Priority Four – Rare Taxa	Taxa which are considered to have been adequately surveyed and which, while being rare (in Australia), are not currently threatened by any identifiable factors.

Results and Discussion

Vegetation associations

Six vegetation associations, including canopy cover variations for 1 of these, were mapped for the Yilliminning Rock reserve (Fig 3). A seventh category, described as a degraded creekline, was also mapped. A description of each association and variants were made and important structural species and generalised understorey descriptions noted (Table 2).

Table 2

Vegetation associations at Yilliminning Rock, including variations and important species.

1: Lithic Complex (granite rock)	<i>Kunzea pulchella</i> , <i>Pimelea graniticola</i> , <i>Borya sphaerocephala</i> , <i>Cheilanthes</i> spp and many herb species.
2: Thicket (granite apron)	<i>Acacia lasiocalyx</i> , <i>Calytrix leschenaultii</i> , <i>Dodonaea</i> spp, <i>Dryandra</i> spp and other shrub species.
3: a, Dense low forest and b, Low forest (granite perimeter)	<i>Allocasuarina huegeliana</i> with scattered <i>Acacia acuminata</i> , <i>A. saligna</i> and <i>Eucalyptus wandoo</i> , with shrub and herbaceous understorey species.
4: Low Woodland	<i>Eucalyptus wandoo</i> with scattered <i>Acacia acuminata</i> and sparse, open shrub understorey.
5: Woodland	<i>Eucalyptus salmonophloia</i> with sub-shrub and herbaceous understorey species
6: Dense heath	<i>Dryandra</i> spp, <i>Melaleuca</i> spp, <i>Isopogon teretifolius</i> with other shrub and herbaceous species.
7: Creek line	Degraded; dominated by <i>Ehrharta calycina</i>

Vegetation on Yilliminning Rock is not uniformly distributed; the shape and slope of the rock are different on all sides. Vegetation usually only associated with granite outcrops occurs on the west side (Association 2; Table 2) dominated by a diversity of flowering shrubs (*e.g.* *Dryandra* and *Dodonaea* spp) and sedges (*e.g.* *Lepidosperma* spp). Crevice and meadow vegetation, also endemic to granite outcrops in the southwest of Western Australia, is scattered across the rock. Steeper parts of the north and western slopes are the exception to this. Distinctive endemics, such as *Kunzea pulchella* and *Baeckea camphorosmae* and *Cheilanthes* ferns, grow in rock crevices (Association 1). Small meadows are also found on Yilliminning Rock comprising *Borya sphaerocephala* and herbaceous endemics such as *Thelmytra antennifera*, *Leporella fimbriata*, *Crassula* spp and *Levenhookia* spp (see also Appendix 1).

Allocasuarina huegeliana forest (Association 3; Table 2) clothes the southern face of Yilliminning Rock to the road to the top (Fig 2). The understorey is primarily herbaceous due to the copious needle litter produced by this tree species. Most notable in this association are 14 species of orchids and numerous species of everlastings. This dense forest association is also found on the northeast side of Yilliminning Rock (Fig 3) where it forms an impenetrable forest with *Acacia saligna* and *Xanthorrhoea brunonis*.

A small but distinctive pocket (about 10 ha) of salmon gum woodland (Association 5; Table 2) lies between the wandoo woodland (Association 4) and rock casuarina forest (Association 3a & 3b; Fig 3). Salmon gum woodland is poorly represented in conservation reserves in the area and this remnant contributes greatly to habitat values of the reserve.

Heath (association 6; Table 2) occupies the northern part of the reserve (Fig 3). It is an important connection to heath on the other side of Birdwhistle Road (Reserve 13343) (Fig 2) and Nature Reserve 17115, approximately 2 km to the northeast.

The creekline (category 7) runs across the southwest of the reserve. It seems not to be degraded native creek vegetation as at other remnants east of the reserve (*unpublished data*) but a drainage channel. *Ehrharta calycina* (veld grass) and *Chenopodium album* (fat hen) dominate the creekline.

Regardless of this, seasonal inundation of stormwater from adjacent farmland, including high levels of nutrients, favour agricultural weeds (e.g. veld grass) which largely replace native species in these low-lying areas.

Flora

Species richness. Granite outcrops in south-west Western Australia are local centres of plant diversity, with high endemism (Hopper *et al.* 1997). Yilliminning Rock fits this model with a high number of species recorded and several known threatened taxa. Appendix 1 lists 238 vascular plant species, including 219 native species, compiled from all vegetation associations (Table 2). Fifty-four families are represented in the list. Appendix 2 lists 33 species of lichens representing 11 families. This diversity of species and communities is high when compared to other woodland reserves in the district (*unpublished data*). Highest numbers of species were recorded from the granite rock crevice, meadow and fringing plant communities, although woodland species are well represented in the species list (Appendix 1).

The seven best represented families at the Yilliminning Rock Reserve (see Appendix 1) were Proteaceae (21), Orchidaceae (19), Asteraceae (17) Myrtaceae (17), Poaceae (16), Papilionaceae (13) and the lichen family Parmeliaceae (16). Genera with the highest number of species were *Acacia* (8), *Hakea* (8), *Dryandra* (6) and *Caladenia* (6) and the lichen genera *Xanthoparmelia* (7).

Priority species. Many populations of priority taxa (Table 1) in the southwest of Western Australia are found outside conservation reserves (Coates & Atkins 1997), and Yilliminning Rock highlights this. Five priority taxa of vascular plants and 2 priority lichens are known to occur in the reserve, as well as species of *Boronia* (*B. aff. subsessilis*) and *Melaleuca* (*aff. scabra*) that are undescribed (see Appendix 1).

- *Caladenia integra*. Priority 4. *C. integra* is known from scattered populations between Tenterden in the south and Clackline in the north, with a disjunct occurrence near Kalbarri (Hoffman & Brown 1992). The southern populations seem to be confined to dense rock sheoak woodlands on and around granite outcrops. *C. integra* was collected (LWS 738) from low sheoak forest (Fig 3) on the reserve in 1996 where it was found to be common.

- *Dryandra fasciculata*. Priority 3. *D. fasciculata* is only known from a few collections in the southern wheatbelt shire of Kulin and further south at Nyabing. A collection was made from a small population in 1996 (LWS 846) in thicket at the base of Yilliminning Rock (Fig 3). The occurrence of this species at Yilliminning Rock extends its known distribution westward by approximately 60 km.

- *Dryandra meganotia*. Priority 3. *D. meganotia* (syn. *D.*

serratuloides subsp. *meganotia*) was recorded from heath on the reserve in 1981 by D Hart (then Department of Fisheries and Wildlife). Since then it has been collected by G Durell in 1995 (GD 98) and by the authors (LWS sn) This species was also found in heath on the adjacent Reserve 13343 (Fig 2). These populations extend the range of *D. meganotia* west, previously only reported from between Kulin and Nyabing (George 1996).

- *Pimelea granitica*. Priority 2. *P. granitica* occurs only on granite outcrops, in soil pockets over granite sheets (Rye 1988). The authors, with S Hopper, collected from 2 new populations (LWS 719 & 840) on Yilliminning Rock in October 1996, each comprising of over one hundred plants, extending the known range west by about 100 km.

- *Stylidium tenuicarpum*. Priority 4. *S. tenuicarpum* is known only from Tutanning Nature Reserve east of Pingelly and the immediate area (Carlquist 1969). The authors, with S Hopper, discovered a new population (LWS 842) on Yilliminning Rock in October 1996.

Lichens. As with other granite outcrops in the wheatbelt, Yilliminning Rock is an important centre of diversity for lichens. A total of 33 lichens, belonging to 11 families have been recorded from the rock. These include 31 species recorded in the Western Australian Herbarium's database WAHERB from a collection made by N Sammy in October 1981 (Appendix 2). Two additional species, *Paraparmelia sammyi* and *P. sargentii* have been recorded by Elix & Johnston (1988) and are listed by the Department of Conservation and Land Management as Priority 2 threatened flora.

Introduced weeds. Only 19 species or 8% of the flora at Yilliminning Rock reserve are introduced weeds. This is lower than ratio's for other remnant woodlands in the area (*unpublished data*). However, many of these are cosmopolitan environmental weeds, some dense in various habitats at Yilliminning Rock, which pose a significant threat to native species and plant communities. The major weeds recorded at Yilliminning Rock are *Avena fatua*, *Briza maxima*, *Ehrharta longiflora*, *E. calycina*, *Freesia leichtlinii* x *alba*, *Hypochoeris glabra*, *Romulea rosea* var *australis* and *Ursinea anthemoides*.

The worst of these is *Freesia leichtlinii* x *alba*, first recorded in 1992 by one of the authors (JPP) at the base of Yilliminning Rock and observed the following year in a crevice on top of the rock. It appears to have invaded from the settlement on the east side Yilliminning Rock (Fig 2) and has now spread through all crevice and meadow vegetation there. Of particular concern is the threat to the newly recorded populations of *Pimelea granitica*. The latter species appears to be an obligate seeder, adapted to a reduced disturbance habitat with minimal competition for resources. The rapid and overwhelming invasion by *Freesia leichtlinii* x *alba* must eventually have a detrimental effect on the recruitment and survival patterns of this and other native species growing in the crevice and meadow communities.

Management issues

Access. There are many management issues at Yilliminning Rock common to most other wheatbelt granite outcrops (see Main 1997) that need to be

addressed. The most significant issues are the control of public access and weeds. Whilst there is no doubt about the importance of public access to the top of the rock, assessment of the current situation is needed to halt the continuing damage to the western face of the rock. Timber has been cut from woodlands in the reserve but some time ago (Anon 1981).

At present, the public is allowed access to the western side of Yilliminning Rock along a graded track from Birdwhistle Rock Road (Fig 2). A small area at the end of this track allows for vehicle turnaround and parking at the base of the rock. A wide and well-worn path is visible up the rockface at this point. Damage over a wide area is a consequence of loose rock being removed or smashed over time. Most lichens and mosses are gone on this part of Yilliminning Rock (Fig 2) and the few meadows left are degraded and weedy. There is also some broken glass and litter about the entry to the rockface from the carpark. A wildfire in 1990, presumably deliberately lit because of its origin and spread, has resulted in weed invasion in this area.

There is also unwanted access off the main entry track north to another part of the rock some 100 m around from the main carpark. Other undesirable car tracks lead north and south from the main track. Salmon gum and wandoo woodland herbfields and soils are sensitive to this kind of damage and it may take years for vehicle tyre marks to disappear. These tracks needed to be closed off with barriers, augmented by the planting of local trees.

Weeds. Weeds invade in response to disturbance and altered environmental conditions. The 1990 wildfire burnt most of the vegetation around the apron on the west side of Yilliminning Rock. Although resprouters dominate these communities, the disturbance allows weeds to establish, particularly in the meadows at the base of the rock and the more open areas of rock casuarina woodland. The common bushland weeds *Hypochoeris glabra* and *Ursinea anthemoides* are prominent here. Another weed, the small sedge *Juncus bufonius*, is common in the granite rock meadows and threatens the stability of this community because of its dense soil seed-bank (*unpublished data*). The most serious weed, *Fresia leichtlinii* x *alba*, has spread rapidly since the early 1990's into much of the low forest and crevice plant communities on the east side of Yilliminning Rock. Immediate measures to control this aggressive weed and monitor its impact on populations of *Pimelea graniticola* are required.

Excess water runoff, which often includes fertilizer from nearby agricultural areas, also provides suitable conditions for weed invasion (Hobbs 1991). One such area, the creekline vegetation in the southwest of the reserve (Fig 3), is infested with grass weeds (e.g. *Ehrharta calycina*). Likewise, the open area at the foot of the northeastern face of Yilliminning Rock, is also heavily infested with grass weeds (e.g. *Avena fatua* and *Bromus diandrus*). This area has been disturbed by unwanted vehicle access also receives high runoff from the steepest part of Yilliminning Rock in winter. Grass weeds at these sites could be controlled with selective herbicides.

Conclusions

Yilliminning Rock is an important local remnant with a broad diversity of habitats and a relatively high level of species richness in vascular plants and lichens. It therefore has high nature conservation value, providing an important link between larger nature reserves to the northeast and the chain of wetland reserves and farm remnants to the southeast, many of which are degraded. The rock itself is of great significance because of its large size and good condition compared to the many degraded granite outcrops on farms in the area, including the nearby Birdwhistle Rock reserve.

A management plan is needed to assist the Narrogin Shire in directing future management Yilliminning Rock (see Anon 1995). Major problems such as access and weed invasion should be addressed. This could be done in as joint consultative project involving the shire, the Department of Conservation and Land Management, the Land Conservation District Committee and other community groups. Part of this process could include public education about ecological issues and the recreation in the Narrogin area, resulting in better management of other remnants.

Acknowledgements: The authors thank K Morris and N Marchant (Science and Information Division, CALM) for supporting this project. The assistance of other CALM staff, G Durrell of the Narrogin District and R Cranfield and T Macfarlane of the Western Australian Herbarium, with information on vascular plant and lichen species is also acknowledged. W Roe provided valuable assistance with field work and an inspection report in 1993. S Hopper of the Kings Park and Botanic Gardens is thanked for accompanying the authors on a field trip in October 1996 and sharing his extensive knowledge of granite rock flora. The thorough collection of lichens made at Yilliminning Rock in 1981 by Mr N Sammy are gratefully acknowledged. A Hopkins, N Gibson and S Hopper made valuable comments on an earlier version of the manuscript.

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Appendix 1

Vascular plant species at Yilliminning Rock Reserve listed by family and with vegetation association from Table 2 and Fig 3; Lithic Complex (1), Thicket (2), Dense Low Forest (3a), Low Forest (3b), Low Woodland (4), Woodland (5) and Dense Heath (6). Introduced species (mostly invasive weeds) are marked *.

Family & species	Vegetation Association
ADIANTACEAE	
<i>Cheilanthes austrotenuifolia</i> H Quirk & TC Chambers	1
<i>C. distans</i> (R Br) Mett	1
<i>C. sieberi</i> Kunze subsp <i>sieberi</i>	1
ASPLENIACEAE	
<i>Pleurosorus rutifolius</i> (R Br) ex Benth	1
JUNCAGINACEAE	
<i>Triglochin calcitrapa</i> Hook	1
POACEAE	
* <i>Aira caryophyllea</i> L	1,2–3
<i>Amphipogon strictus</i> R Br	3,4
<i>A. turbinatus</i> R Br	3,4
<i>Austrostipa elegantissima</i> (Labill SWL) Jacobs & J Everett	1,2–3,4
<i>A. semibarata</i> Labill	5
* <i>Avena fatua</i> L	1,2,3
* <i>A. sativa</i> L	2–3
* <i>Briza maxima</i> L	1,4
* <i>B. minor</i> L	1,4
* <i>Bromus diandrus</i> Roth	1
* <i>Ehrharta calycina</i> Smith	4 & creekline
* <i>E. longiflora</i> Smith	4
* <i>Lolium rigidum</i> Gaudin	2–3
<i>Neurachne alopecuroides</i> R Br	2–3,6
<i>Notodanthonia caespitosa</i> (Gaudich) Zotov	5
<i>Spartochloa scirpoidea</i> (F Muell) Maiden & E Betche	1
* <i>Vulpia myuros</i> (L) C Gmelin	1,4
CYPERACEAE	
<i>Caustis dioica</i> R Br	2–3,5
<i>Gahnia australis</i> (Nees) KL Wilson	2–3,5
<i>Lepidosperma gracile</i> R Br	2–3
<i>L. pruinatum</i> Kuek	6
<i>L. resinosum</i> (Nees) Benth	2–3,5
<i>Mesomelaena stygia</i> (R Br) Nees aff subsp <i>stygia</i>	4
<i>Schoenus brevifolius</i> (R Br) Benth	6
RESTIONACEAE	
<i>Desmodcladus flexuosa</i> (R Br) LAS Johnson & BG Briggs ms	2–3
<i>Desmodcladus</i> sp (JPP sn)	5

CENTROLEPIDACEAE	
<i>Aphelia brizula</i> F Muell	2–3
<i>Centrolepis aristata</i> (R Br) Roemer & Schultes	2–3
<i>Centrolepis pilosa</i> Hieron	2–3
<i>C. polygyna</i> (R Br) Hieron	1
JUNCACEAE	
* <i>Juncus bufonius</i> L	1
ANTHERICACEAE	
<i>Arthropodium capillipes</i> Endl	1,2–3
<i>Borya sphaerocephala</i> R Br	1, 2,3
<i>Caesia parviflora</i> R Br	2–3
<i>Chamaescilla corymbosa</i> (R Br) F Muell ex Benth	2–3,4
<i>Laxmannia squarrosa</i> Lindley	2–3
<i>L. grandiflora</i> Lindley	4
<i>Sowerbaea laxiflora</i> Lindley	2–3,4
<i>Thysanotus patersoni</i> R Br	1,2–3
DASYPOGONACEAE	
<i>Lomandra effusa</i> (Lindley) Ewart	5
<i>L. micrantha</i> (Endl) Ewart	5
<i>L. rupestris</i> (Endl) Ewart	3b
<i>L. suaveolens</i> (Endl) Ewart	4
<i>Lomandra</i> sp (LWS 724)	3
XANTHORRHOACEAE	
<i>Xanthorrhoea brunonis</i> Endl In Lehm	2–3,6
PHORMIACEAE	
<i>Dianella revoluta</i> R Br	4
<i>Stypandra glauca</i> R Br	1,2–3
HAEMODORACEAE	
<i>Anigozanthos humilis</i> Lindley	2–3,6
<i>Conostylis aculeata</i> R Br subsp <i>bromeloides</i> (Endl) JW Green	2–3
<i>C. pusilla</i> Endl	2–3,4
<i>C. setiga</i> R Br	2–3
<i>Haemodorum laxum</i> R Br	2–3
<i>H. aff paniculatum</i> (JPP sn)	4
IRIDACEAE	
* <i>Freesia leichtlinii</i> Klatt x <i>alba</i>	1,2,3,5
<i>Orthrosanthus laxus</i> (Endl) Benth	2–3
<i>Patersonia juncea</i> Lindley	2–3
* <i>Romulea rosea</i> (L) Ecklon	1,4
ORCHIDACEAE	
<i>Burnettia nigricans</i> (R Br) Hopper & Brown	2–3,4
<i>Caladenia chapmanii</i> ms (LWS 740,742,743,744)	2–3,1,4
<i>C. falcata</i> (Nicholls) MAClem & Hopper	2–3
<i>C. flava</i> R Br	2–3,1,4
<i>C. hirta</i> Lindley subsp <i>hirta</i> ms (LWS 747)	4
<i>C. integra</i> E Coleman	2–3,1
<i>C. longicauda</i> Lindley subsp <i>eminens</i> ms (LWS 745)	4
<i>Cyanicula deformis</i> (R Br)	2–3
<i>C. gemmata</i> (Lindley) Hopper & Brown	1
<i>Diuris corymbosa</i> Lindley	2–3,4
<i>Diuris</i> sp (JPP sn)	2–3
<i>Eriochilus dilatatus</i> Lindl	5
<i>Leporella fimbriata</i> (Lindl) AS George	5
<i>Pterostylis hamiltonii</i> Nicholls	2–3
<i>P. recurva</i> Benth	2–3
<i>P. sanguinea</i> DL Jones & MA Clem	4
<i>Spiculaea ciliata</i> Lindley	1
<i>Thelymitra nuda</i> R Br	1
<i>T. antennifera</i> (Lindley) JD Hook	1
CASUARINACEAE	
<i>Allocasuarina huegeliana</i> (Miq) L Johnson	2–3,4
<i>A. microstachya</i> (Miq) L Johnson	2–3,1
PROTEACEAE	
<i>Adenanthos cygnorum</i> Diels aff subsp <i>cygnorum</i>	6
<i>Banksia sphaerocarpa</i> R Br var <i>sphaerocarpa</i>	6
<i>Conospermum stoehadis</i> Endl subsp <i>sclerophyllum</i> (Lindl) EM Benn	2–3
<i>Dryandra armata</i> R Br	6

<i>D. fasciculata</i> AS George	2-3	<i>G. spinosum</i> Benth var <i>spinosum</i>	2-3,4
<i>D. fraseri</i> R Br var <i>fraseri</i>	5	<i>Gompholobium marginatum</i> R Br	2-3,4
<i>D. meganotia</i> AS George	6	<i>Isotropis cuneifolia</i> (Smith) Benth ex BD Jackson	4
<i>D. nivea</i> (Labill) R Br subsp <i>nivea</i>	2-3	<i>Jacksonia aff sternbergiana</i> Huegel	6
<i>D. squarrosa</i> R Br subsp <i>squarrosa</i>	2-3	<i>J. eremodendron</i> E Pritz	6
<i>Grevillea pilulifera</i> (Lindley) Druce	2-3	<i>Sphaerolobium medium</i> R Br	2-3
<i>Hakea amplexicaulis</i> R Br	2-3	<i>Templetonia sulcata</i> (Meissner) Benth	5
<i>H. baxteri</i> R Br	6	GERANIACEAE	
<i>H. incrassata</i> R Br	6	* <i>Erodium botrys</i> (Cav) Bertol	1
<i>H. lissocarpa</i> R Br	5	RUTACEAE	
<i>H. petiolaris</i> Meissner	2-3	<i>Boronia</i> sp nov LWS 836 (aff <i>B. subsessilis</i>)	2-3
<i>H. prostrata</i> R Br	5	TREMANDRACEAE	
<i>H. trifurcata</i> (Smith) R Br	2-3	<i>Tetralheca hirsuta</i> Lindley	2-3,4
<i>H. undulata</i> R Br	2-3	POLYGALACEAE	
<i>Isopogon teretifolius</i> R Br	6	<i>Comesperma ciliatum</i> Steetz	2-3
<i>Persoonia trinervis</i> Meissner	2-3	<i>C. scoparium</i> Steetz	2-3
<i>Petrophile squamata</i> R Br	2-3,6	EUPHORBIACEAE	
<i>Synaphea petiolaris</i> R Br	2-3	<i>Poranthera microphylla</i> Brongn	2-3
<i>Synaphea</i> sp (Pieroni 14)	4	STACKHOUSIACEAE	
SANTALACEAE		<i>Stackhousia luegelii</i> Endl	2-3
<i>Choretrum glomeratum</i> R Br var <i>glomeratum</i>	4	<i>S. pubescens</i> A Rich	2-3
<i>Exocarpos aphyllus</i> R Br	5	SAPINDACEAE	
<i>Leptomeria pauciflora</i> R Br	2-3	<i>Dodonaea viscosa</i> Jacq subsp <i>spathulata</i>	1,4
<i>L. spinosa</i> (MIQ) A DC	2-3	<i>D. pinifolia</i> Miq	2-3
<i>Santalum acuminatum</i> (R Br) A DC	2-3	RHAMNACEAE	
LORANTHACEAE		<i>Cryptandra nutans</i> Steud	2-3
<i>Anyema miquelii</i> (Miq) Tiegh	4,5	<i>C. pungens</i> Steud	2-3
GYROSTEMONACEAE		<i>Cryptandra</i> sp (LWS 710)	3
<i>Gyrostemon subnudus</i> (Nees) Baill	2-3	STERCULIACEAE	
CHENOPODIACEAE		<i>Thomasia foliosa</i> Gay	2-3
<i>Atriplex exilifolia</i> F Muell	4-5	DILLENIACEAE	
* <i>Chenopodium album</i> L	4 & creekline	<i>Hibbertia acerosa</i> (R Br ex DC) Benth	2-3
PORTULACACEAE		<i>H. exasperata</i> (Steudel) Briq	4
<i>Calandrinia calyptata</i> JD Hook	1	<i>H. rupicola</i> (S Moore) C Gardner	2-3
CARYOPHYLLACEAE		STYLIDIACEAE	
* <i>Petrohragia velutina</i> (Guss) P Ball	1	<i>Levenhookia dubia</i> Sonder	1
LAURACEAE		<i>L. pusilla</i> R Br	1
<i>Cassytha aurea</i> JZ Weber var <i>hirta</i>	2-3	<i>Stylidium calcaratum</i> R Br	1
DROSERACEAE		<i>S. ecorne</i> (F Muell ex R Erickson & JH Willis)	1
<i>Drosera glanduligera</i> Lehm	1,2-3	PG Farrell & SH James	1
<i>D. macrantha</i> Endl subsp <i>macrantha</i>	1,4,5	<i>S. petiolare</i> Sonder	2-3
<i>D. menziesii</i> R Br subsp <i>menziesii</i>	2,3,4	<i>S. piliferum</i> R Br	1
<i>D. aff pycnoblata</i> (LWS 717)	5	<i>S. tenuicarpum</i> Carlq	2-3
<i>D. aff gigantea</i> (LWS 715)	1,2-3	THYMELIACEAE	
CRASSULACEAE		<i>Pimelea graniticola</i> Rye	1
<i>Crassula closiana</i> (Gay) Reiche	1	<i>P. rosea</i> R Br	2-3
<i>C. decumbens</i> Thunb var <i>decumbens</i>	1	MYRTACEAE	
* <i>C. natans</i> Thunb var <i>minus</i>	1	<i>Baeckea camphorosmae</i> Endl	2-3
PITTOSPORACEAE		<i>B. crispiflora</i> F Muell	5
<i>Sollya heterophylla</i> Lindley	5	<i>Baeckea</i> sp Narrogin (R Hnatiuk 780011)	2-3
MIMOSACEAE		<i>Calothamnus quadrifidus</i> R Br	2-3
<i>Acacia acuminata</i> Benth	2-3,4,5	<i>Calytrix leschenaultii</i> (Schauer) Benth	2-3
<i>A. erinacea</i> Benth	5	<i>Eucalyptus salmonophloia</i> F Muell	5
<i>A. lasiocarpa</i> var <i>sedifolia</i> (Meisn) Maslin	4	<i>E. rudis</i> Endl	4 (N only)
<i>A. lasiocalyx</i> CRP Andrews	2-3	<i>E. wandoo</i> Blakely	3,4,5
<i>A. microbotra</i> Benth	3,4	<i>Kunzea pulchella</i> (Lindley) AS George	1,2-3
<i>A. pulchella</i> R Br	5	<i>K. recurva</i> Schauer in Lehm	6
<i>A. saligna</i> (Labill) HL Wendl	2-3	<i>Leptospermum erubescens</i> Schauer in Lehm	2-3
<i>A. stenoptera</i> Benth	4,5	<i>Leptospermum</i> sp (LWS 838)	
<i>Acacia</i> sp (LWS 716)	2-3	<i>Melaleuca pungens</i> Schauer in Lehm	6
<i>Acacia</i> sp (BR Maslin 6754)	4	<i>M. scabra</i> R Br	5
<i>Acacia</i> sp (BR Maslin 6757)	6	<i>M. undulata</i> Benth	6
PAPILIONACEAE		<i>M. sp nov</i> LWS 987 (<i>M. scabra</i> group)	5
<i>Bossiaea eriocarpa</i> Benth	4	<i>Thryptomene australis</i> Endl	1
<i>Daviesia cardiophylla</i> F Muell	2-3,6	<i>Verticordia endlicheriana</i> Schauer	2-3,6
<i>D. hakeoides</i> Meisn subsp <i>hakeoides</i>	2	<i>V. grandiflora</i> Endl	2-3,5
<i>D. preissii</i> Meissner	2-3,5	<i>V. insignis</i> Endl subsp <i>compta</i>	6
<i>D. uncinata</i> Crisp	6	<i>V. plumosa</i> (Desf) Druce	6
<i>Gastrolobium calycinum</i> Benth	4		

HALORAGACEAE	
<i>Glischrocaryon aureum</i> (Lindley) Orch var <i>aureum</i>	1,2-3
<i>Gonocarpus nodulosus</i> Nees	1
APIACEAE	
<i>Hydrocotyle</i> sp	2-3
<i>Trachymene ornata</i> (Endl) Druce	1
<i>T. pilosa</i> Smith	2-3,1
EPACRIDACEAE	
<i>Astroloma</i> aff <i>drummondii</i> Sonder	2-3,5
<i>A. pallidum</i> R Br	5
<i>Leucopogon dielsianus</i> E Pritzel	4, 6
<i>Lysinema ciliatum</i> R Br	2-3,4
PRIMULACEAE	
* <i>Anagallis arvensis</i> L	2-3
LOGANIACEAE	
<i>Logania</i> sp (JPP sn)	2-3
<i>Mitrasacme paradoxa</i> R Br	2-3
VERBENACEAE	
<i>Halgania</i> sp (JPP sn)	2-3
SOLANACEAE	
<i>Nicotiana rotundifolia</i> Lindl	1
SCROPHULARIACEAE	
* <i>Parentucellia latifolia</i> (L) Caruel	2,3
MYOPORACEAE	
<i>Eremophila</i> aff <i>glabra</i> (LWS 729)	5
RUBIACEAE	
<i>Opercularia vaginata</i> Labill	2-3
GOODENIACEAE	
<i>Dampiera alata</i> Lindley	2-3
<i>D. lavandulacea</i> Lindl	5
<i>D. lindleyi</i> Vriese	2-3
<i>Goodenia helusii</i> (E. Pritz) Carolin	1
<i>G. micrantha</i> Hemsl ex Carolin	1, 2-3
<i>G. pulchella</i> Benth	1,2
<i>Lechenaultia biloba</i> Lindley	6
ASTERACEAE	
<i>Brachycome ibiderifolia</i> Benth	2-3,4,5
<i>B. perpusilla</i> (Steetz) J Black	1, 2-3
<i>Gnephosis tenuissima</i> Cass	2-3
<i>Helichrysum leucopsidium</i> DC	5
<i>Helipterum laeve</i> (A Gray) Benth	5
<i>Hyaospermum demissum</i> (A Gray) PG Wilson	1
* <i>Hypochaeris glabra</i> L	1,2-3,4
<i>Lagenifera huegelii</i> Benth in Endl	2-3
<i>Podolepis canescens</i> Cunn Ex DC	5
<i>P. lessonii</i> (Cass) Benth	2-3,5
<i>Podotheca angustifolia</i> (Labill) Less	2-3
<i>Quinetia urvillei</i> Cass	2-3
<i>Rhodanthe manglesii</i> Lindley	2-3
* <i>Ursinia anthemoides</i> (L) Poiret	2-3,1,4
<i>Waitzia acuminata</i> Steetz	5
<i>W. citrina</i> (Benth) Steetz	2-3

Appendix 2

Lichen species, arranged by family, recorded at Yilliminning Rock near Narrogin, Western Australia

Family & species

ACAROSPORACEAE

Acarospora schleicheri (Ach) Mass (syn *A. citrina*)

CLADIACEAE

Cladia aggregata (Sw) Nyl

C. ferdinandii (Mull Arg) R Filson

DICRANACEAE

Campylopus australis Catches & Frahm

C. bicolor (C. Muell.) Hook f & Wils

HETERODACEAE

Heterodea muelleri (Hampe) Nyl

LECIDEACEAE

Lecidea laeta Stirton

Lecidea sp (N Sammy 840850)

Toninia sp (N Sammy 840848)

PARMELIACEAE

Canoparmelia pruinata (Mull Arg) Elix & Johnston

Flavoparmelia rutidota (JD Hook & Taylor) Hale

Neofuscelia imitatrix (Taylor) Esslinger

N. incantata (Esslinger) Esslinger

N. pulla (Ach) Esslinger

Paraparmelia samuui Elix & Johnston

P. sargentii Elix & Johnston

Punctelia subalbicans (Stirton) Galloway & Elix

Rhizocarpon sp (N Sammy 840860)

Xanthoparmelia concomitans Elix & Johnston

X. eiliffii Elix & Johnston

X. flavescens (Gyelnik) Galloway

X. notata (Kurokawa) Hale

X. reptans (Kurokawa) Elix & Johnston

X. substrigosa (Hale) Hale

X. tasmanica (JD Hook & Taylor) Hale

PHYSICIACEAE

Buellia sp (N Sammy 840862)

P. tribacia (Ach) Nyl

Physcia aipolia (Ehrh ex Humb) Furnrohr

SIPHULACEAE

Siphula coriacea Taylor ex Nyl

TELEOSCHISTACEAE

Caloplaca sp (N Sammy 840861)

THELOTREMACEAE

Diploschistes australasicus Lumbsch & Elix

Diploschistes sp (JA Elix 41042)

VERRUCARIACEAE

Endocarpon sp (N Sammy 840825, 840826, 840827)

Why is *Santalum spicatum* common near granite rocks?

J E D Fox

School of Environmental Biology, Curtin University, GPO Box 1987, Perth WA 6001
email: rfoxjed@cc.curtin.edu.au

Abstract

Sandford Rocks Nature Reserve is dominated by a large granite outcrop. This reserve is notably well-endowed with trees of the root parasite sandalwood (*Santalum spicatum*). These are comparatively common in and among granite exposures. Trees attain 4 m in height and 20 cm basal diameter on favourable sites but are small gnarled shrubs in rock fissures. Fruiting ability differs considerably between trees. Despite apparently high densities of rabbits, continuous regeneration appears to have occurred, but only in the vicinity of parent trees. The reserve contains a number of distinct vegetation associations that are soil determined. Although sandalwood is common near exposed granite it is rarely found in association with *Eucalyptus* stands. It is suggested that the water-shedding properties of the granite exposures are less important to sustaining sandalwood than the presence of preferentially parasitised host species.

Introduction

Most investigations of parasitism have been concerned with relatively short lived species (Matthies 1995) and although parasitic plants may have major impacts on structure and dynamics of natural vegetation (Pennings & Callaway 1996), little is known of their regeneration. Confirmation that particular host species can enable long-lived parasitic plants to perform better under field conditions is time consuming but a necessary prerequisite if such species are to be cultivated (Fox *et al.* 1996). Perennial woody semi-parasites tend to have larger seed (Musselman & Mann 1978) than invasive shrubs (Grice 1996) and longer-lived perennials are likely to have temporally distinct growth phases.

In much of the eastern wheatbelt of Western Australia the obligate semi-parasitic small tree sandalwood (*Santalum spicatum* [R Br] A DC) is now uncommon. This species was the most valuable natural product to settlers and was severely exploited from about the turn of the century after the railway reached Southern Cross in 1894 (Loneragan 1990) and is now absent from some areas (Lange 1960). It remains an important and valuable resource in more arid regions of the State, accounting for some \$7 million in royalties paid to the Department of Conservation and Land Management in 1993-94. That represents some 22 % of all royalty revenue, only marginally less than that from woodchips (Anon 1994). A management plan for sandalwood was prepared in 1991 (Kealley 1991). Little is known of the impact of *S. spicatum* on natural plant communities.

Study Area and Methods

Sandford Rock Nature Reserve (SRNR) lies 9 km north east of the small town of Westonia (31° 15' S, 118° 45' E). Curtin University has undertaken research into the vegetation of the reserve since 1991. The family

Santalaceae is represented by three small tree species: *Exocarpos aphyllus* R Br (leafless ballart), *Santalum acuminatum* (R Br) A DC (quandong) and *Santalum spicatum* (sandalwood). The latter is known to parasitise a number of potential hosts, usually including acacias (e.g. *A. acuminata* Benth, *A. aneura* F Muell ex Benth, and *A. tetragonophylla* F Muell), *Allocasuarina*, *Melaleuca* and some herbaceous species. Eucalypts are not considered to be good hosts (Barrett & Fox 1995). Eight of 17 species recorded as hosts to *Santalum spicatum* by Loneragan (1990) occur at SRNR. The Reserve contains at least 14 species of *Eucalyptus*, 4 species of *Allocasuarina* and 9 species of *Melaleuca* (Fox *et al.* 1993). Up to 25 species of *Acacia* occur, often in well-defined habitats. These numbers compare with those of Hopper *et al.* (1997) of 83 *Acacia* and 25 *Melaleuca* for granite outcrops generally.

The climatic regime is described by Beard (1981) as extra dry mediterranean. The mean annual rainfall is around 330 mm and some summer rain is usually experienced (Fig 1). Water shed from the massive complex of granite occupying the centre of the reserve

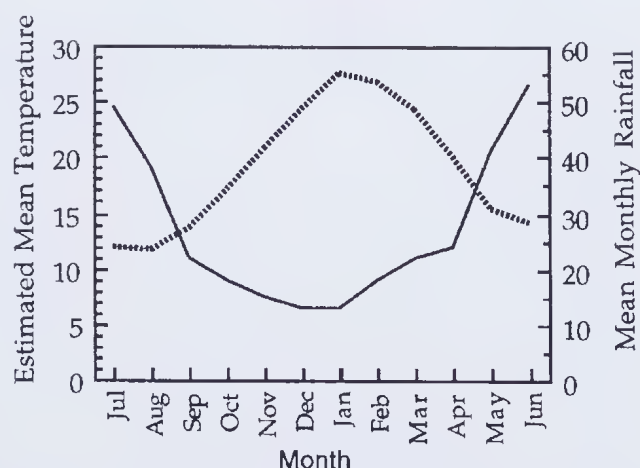


Figure 1. Estimated mean temperature (°C; broken line) and mean monthly rainfall (mm; solid line) for the study area near Westonia.

fills rock pools in winter, drives an ephemeral stream and probably contributes to underground aquifers supplying eucalypt stands of the area through the drier months.

SRNR occupies a land area of ~800 ha (Fig 2). On and around the granite exposures, soil pockets of variable depth occur, with heath or shrubland while the surrounding flats carry shrublands or woodlands. Within the reserve a mosaic of soil types is reflected in the dominating suites of plant species. The vegetation is described by Muir (1979) as jam woodland on moderately well-drained pinkish grey, gritty loam; gimlet woodland on poorly drained red, sandy clay; wandoo (with scattered salmon gum) and York gum woodland mainly on poorly drained pinkish grey, sandy clay loam; mallee with *Acacia acuminata* and *A. stereophylla* Meissner in Lehm, on light reddish brown, loams and *Acacia hemiteles* Benth on areas of heavier soil, poorly drained, of pinkish grey, sandy clay. Tamma shrubland is present (*Allocasuarina campestris* (Diels) L Johnson or *A. acutivalvis* (F Muell) L Johnson) with *Acacia stereophylla* locally co-dominant. Tamma soils are well-drained brownish yellow, fine sandy loams, with 40–60% laterite in some areas. Granitic soils at SRNR are similar to those at Durokoppin Nature Reserve (31 °

23' S, 117 ° 46' E) described by McArthur (1991). The Southern Cross mallee (*Eucalyptus crucis* Maiden) occurs in thickets of myrtaceous scrub in relatively deep and well watered soil around the edges of the exposed rock. Fire has not occurred in SRNR since at least 1927 (Fox *et al.* 1993).

Reconnaissance indicated that sandalwood trees are frequent in 4 general localities (Fig 2). The first, PA, is in the vicinity of a picnic site in the south west. Here, sandalwood occurs in low mixed woodland, among and adjacent to *Acacia* species and *Allocasuarina huegeliana* (Miq) Johnson, near an ephemeral stream. The second, to the north and east of PA, covers several loosely defined areas (with the prefix R). These areas lie adjacent to large granite exposures and are mainly associated with narrow bands of mixed woodland (R) or *Allocasuarina huegeliana* (RE). One set is to the south of a major overhang (RO); another (RS), is associated with thickets of *Leptospermum erubescens* Schauer in Lehm. The third and fourth localities are further north and lie between major rock exposures; in one case (CK 3) adjacent to dense stands of eucalypt woodland, and in the second, among patches of *Allocasuarina huegeliana* and adjacent to another rock exposure (CK 3B).

At these localities, sandalwood trees have been

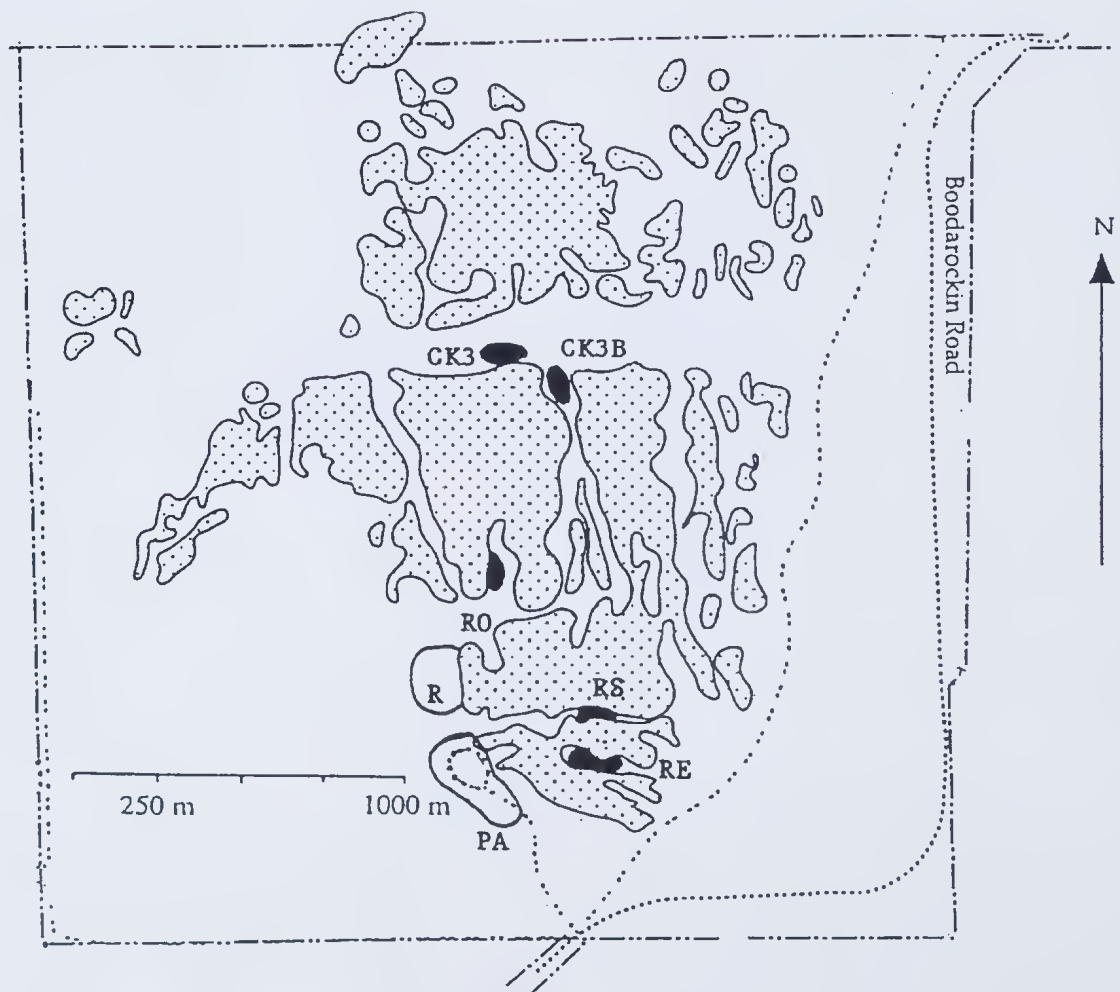


Figure 2. Plan of the Sandford Rocks Nature Reserve, showing sandalwood sample areas.

mapped and measured for height, crown widths and stem diameters at 5, 15 and 130 cm above ground level. Observations on flowering have been made and fallen nuts from the previous years' crops have been counted in March. Soil depth in the vicinity of sandalwood trees has been obtained from a mean of 3 probes. Adjacent perennial species have been recorded. Sandalwood seedlings are counted when present.

Results

Stocking

Most measured trees are 200– 400 cm tall (70 %), with only 10 of 161 enumerated in 1996 of > 400 cm in height (Table 1). Mean heights by localities at March 1996 are; PA- 258 cm ± se 13 (n= 39); CK3- 244 cm ± se 10 (n= 54); CK3B- 301 cm ± se 17 (n= 34); and R- 265 cm ± se 16 (n= 34). Distribution within 50 cm height classes is illustrated (Fig 3). The whole population has a normal height class distribution but the four localities differ. R trees depart most from normal distribution with two peaks. The

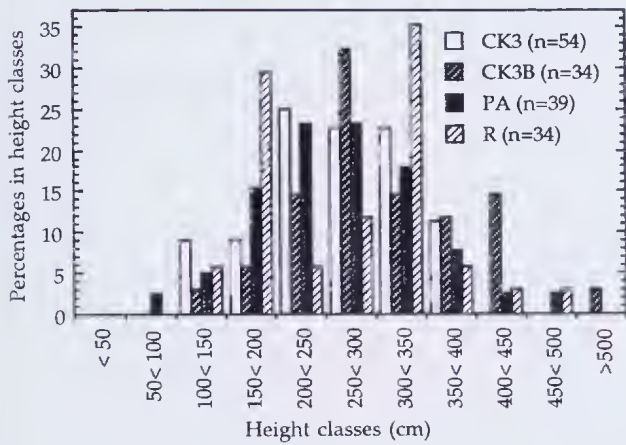


Figure 3. Plants closest to the rocks are less normally distributed in height class than those further away.

small spread of heights at CK3 probably reflects inter-plant competition. The high proportion of taller trees at CK3B may indicate best growing conditions.

Mean stocking of sandalwood on 5.83 ha sampled (excluding area R where trees are scattered individuals across a large area) is 26.1 trees ha⁻¹. The density of sandalwood trees is very variable. For the 2.5 ha of woodland sampled at PA, where no tree is near any exposed granite, and all lie west of the stream, the mean number of trees is 15.6 ha⁻¹ (Table 1). On the rocky sites, where the area taken is that occupied by trees and shrubs, stocking varies from 5.5 ha⁻¹ on 2 ha constituting the east patch of *Allocasuarina huegeliana* (RE), through 18 ha⁻¹ on 0.33 ha of mainly *Leptospermum erubescens* thicket (RS), to 40 ha⁻¹ on the 0.2 ha of mixed vegetation at RO. Stocking is highest at the localities adjacent to granite: 180 ha⁻¹ on 0.3 ha at CK3 and 68 ha⁻¹ on 0.5 ha at CK3B.

Sandalwood trees tend to be grouped and at each of PA, CK3 and CK3B clumps of 4–30 trees are treated separately as subsets (Table 1). These clumps occupy areas of 40 to 100 m² and have local densities of 400–3 000 trees ha⁻¹. Seedlings (sandalwoods generally <150 cm tall) also tend to be clumped and are not currently found away from parent trees.

Hosts

Some 48 different perennial plant species from 23 families occur in the vicinity of the measured sandalwood trees taken as 110 individuals or clumps (Table 2). Those listed include most of the important perennials found in vegetation adjacent to sandalwood at the four localities examined. The species *Acacia acuminata*, *Dianella revoluta*, *Dodonaea inaequifolia* and *Allocasuarina huegeliana* appear most frequently. The localities differ, with more species recorded at R sites (31 species; mean species per sandalwood 3.5) and least at PA and CK3 (14 species; mean species per sandalwood 3 and 2.5 respectively). Locality CK3B, with 24 species has most co-occurrences per sandalwood (8).

Despite the large number of *Acacia* species present in SRNR, only *A. acuminata* appears to be important as a potential host. It is the most frequent species at 3 of the 4

Table 1
Stocking data for designated sample areas at Sandford Rock Nature Reserve.

Locality ¹	Sample area ² (m ²)	Seedlings ³	Number of sandalwoods by height classes (cm)				Number ha ⁻¹	
			< 200	200-300	300-400	>400	Trees only	All plants
PA	25 000	63	9	18	10	2	15.6	40.8
Sub-set a	50	0	2	5	1	1	1 800	1 800
Sub-set b	40	36	0	5	0	0	1 250	10 250
R	diffuse ⁴	56	3	3	3	0	nc ⁴	nc ⁴
RE	20 000	0	4	3	4	0	5.5	5.5
RS	3 333	0	4	0	2	0	18	18
RO	2 000	9	1	0	5	2	40	85
CK3	3 000	41	15	24	15	0	180	316
Sub-set a	100	30	7	15	8	0	3 000	6 000
CK3B	5 000	119	3	16	9	6	68	306
Sub-set a	100	29	0	1	1	2	400	3 300

¹ See Figure 2 for localities. ² The sub-sets represent small areas of concentrated *Santalum spicatum* plants. ³ Seedlings generally < 150 cm tall. ⁴ nc= not calculated

Table 2

Frequency of occurrence of 110 trees or clumps of *Santalum spicatum* with other perennial species at 4 localities within Sandford Rocks Nature Reserve; number (#) and percentage (%).

Possible host species (ranked alphabetically in order of frequency)	Family	Life form	Locality [as in Table 1]								All as % (n= 110)
			R (n= 34)		CK 3 (n=17)		CK 3B (n=32)		PA (n= 27)		
			#	%	#	%	#	%	#	%	
<i>Acacia acuminata</i> Benth	Mimosaceae	Tree	10	29	15	88	25	78	18	67	62
<i>Dianella revoluta</i> R Br	Phormiaceae	Herbaceous	7	21	2	12	28	88	1	4	35
<i>Dodonaea inaequifolia</i> Turcz	Sapindaceae	Medium shrub	11	32	1	6	12	38	14	52	35
<i>Allocasuarina huegeliana</i> (Miq) L Johnson	Casuarinaceae	Tree	9	26	2	12	25	78	–	–	33
<i>Dodonaea viscosa</i> Jacq	Sapindaceae	Medium shrub	14	41	–	–	17	53	–	–	28
<i>Comesperma volubile</i> Labill	Polygalaceae	Twiner	2	6	–	–	19	59	–	–	19
<i>Chamaexeros fimbriata</i> (F Muell) Benth	Dasypogonaceae	Herbaceous	8	24	–	–	12	38	–	–	18
<i>Eucalyptus loxophleba</i> Benth	Myrtaceae	Mallee	1	3	1	6	3	9	15	56	18
<i>Hibbertia glomerosa</i> (Benth) F Muell	Dilleniaceae	Low shrub	–	–	–	–	20	63	–	–	18
<i>Lepidosperma gracile</i> R Br	Cyperaceae	Sedge	4	12	–	–	13	41	1	4	16
<i>Stipa elegantissima</i> Labill	Poaceae	Grass	–	–	–	–	18	56	–	–	16
<i>Allocasuarina campestris</i> (Diels) L Johnson	Casuarinaceae	Medium shrub	2	6	2	12	13	41	–	–	15
<i>Alyxia buxifolia</i> R Br	Apocynaceae	Tall shrub	1	3	–	–	6	19	9	33	15
<i>Calothamnus asper</i> Turcz	Myrtaceae	Medium shrub	3	9	5	29	5	16	–	–	12
<i>Hakea recurva</i> Meissner in DC	Proteaceae	Medium shrub	3	9	–	–	–	–	8	30	10
<i>Leptospermium crubescens</i> Schauer in Lehm	Myrtaceae	Medium shrub	7	20	4	24	–	–	–	–	10
<i>Melaleuca hamulosa</i> Turcz	Myrtaceae	Tall shrub	–	–	3	18	6	19	–	–	8
<i>Melaleuca radula</i> Lindley	Myrtaceae	Medium shrub	–	–	2	12	7	22	–	–	8
<i>Lepidosperma drummondii</i> Benth	Cyperaceae	Sedge	8	23	–	–	–	–	–	–	7
<i>Solanum nummularium</i> S Moore	Solanaceae	Low shrub	2	6	–	–	6	19	–	–	7
<i>Stypandra imbricata</i> R Br	Phormiaceae	Herbaceous	1	3	–	–	6	19	–	–	6
<i>Eucalyptus capillosa</i> Brooker & Hopper	Myrtaceae	Tree	–	–	1	6	–	–	4	15	5
<i>Grevillea paniculata</i> Meissner in Lehm	Proteaceae	Medium shrub	5	15	–	–	–	–	–	–	5
<i>Hibbertia exasperata</i> (Steudel) Briq	Dilleniaceae	Low shrub	6	18	–	–	–	–	–	–	5
<i>Keraudrenia integrifolia</i> Steudel in Lehm	Sterculiaceae	Low shrub	–	–	–	–	5	16	–	–	5
<i>Rhagodia drummondii</i> Moq in DC	Chenopodiaceae	Low shrub	–	–	–	–	5	16	–	–	5
<i>Acacia hemiteles</i> Benth	Mimosaceae	Medium shrub	–	–	–	–	–	–	4	15	4
<i>Solanum lasiophyllum</i> Dunal ex Poiret	Solanaceae	Low shrub	–	–	–	–	3	9	1	4	4
<i>Spartochloa scirpoidea</i> (Steudel) C E Hubb	Poaceae	Grass	4	12	–	–	–	–	–	–	4
<i>Acacia erinacea</i> Benth	Mimosaceae	Low shrub	1	3	–	–	–	–	2	7	3
<i>Allocasuarina acutivalvis</i> (F Muell) L Johnson	Casuarinaceae	Medium shrub	–	–	–	–	3	9	–	–	3
<i>Cassia nemophila</i> Cunn ex Vogel	Caesalpiniaceae	Medium shrub	2	6	1	6	–	–	–	–	3
<i>Daviesia nematophylla</i> F Muell ex Benth	Papilionaceae	Medium shrub	–	–	–	–	3	9	–	–	3
<i>Scaevola spinescens</i> R Br	Goodeniaceae	Low shrub	–	–	–	–	–	–	3	11	3
<i>Solanum orbiculatum</i> Dunal	Solanaceae	Low shrub	–	–	–	–	3	9	–	–	3
<i>Acacia colletioides</i> Benth	Mimosaceae	Tall shrub	–	–	–	–	–	–	2	7	2
<i>Acacia saligna</i> (Labill) Wendl	Mimosaceae	Tall shrub	2	6	–	–	–	–	–	–	2
<i>Astroloma serratifolium</i> (DC) Druce	Epacridaceae	Low shrub	2	6	–	–	–	–	–	–	2
<i>Melaleuca macronychia</i> Turcz	Myrtaceae	Medium shrub	1	3	1	6	–	–	–	–	2
<i>Olearia revoluta</i> F Muell ex Benth	Asteraceae	Low shrub	–	–	2	12	–	–	–	–	2
<i>Baeckea behrii</i> (Schldl) F Muell	Myrtaceae	Tall shrub	1	3	–	–	–	–	–	–	<1
<i>Billardiera crubescens</i> (Putterl) E M Bennett	Pittosporaceae	Twiner	1	3	–	–	–	–	–	–	<1
<i>Eremophila scoparia</i> (R Br) F Muell	Myoporaceae	Low shrub	1	3	–	–	–	–	–	–	<1
<i>Eucalyptus crucis</i> Maiden	Myrtaceae	Tree	1	3	–	–	–	–	–	–	<1
<i>Melaleuca uncinata</i> R Br in W T Aiton	Myrtaceae	Tall shrub	–	–	–	–	1	3	–	–	<1
<i>Persoonia striata</i> R Br	Proteaceae	Medium shrub	1	3	–	–	–	–	–	–	<1
<i>Pittosporum phylliracoides</i> DC	Pittosporaceae	Tree	–	–	–	–	–	–	1	4	<1
<i>Pityrodia teckiana</i> (F Muell) E Pritzel	Chloanthaceae	Low shrub	1	3	–	–	–	–	–	–	<1

Botanical nomenclature after Green (1985). Life forms: tree – a single stem; mallee – multi-stemmed *Eucalyptus*; tall shrub – mature individuals > 2m in height; medium shrub – mature individuals > 1 m tall, but not > 3 m; low shrub – generally < 1 m tall.

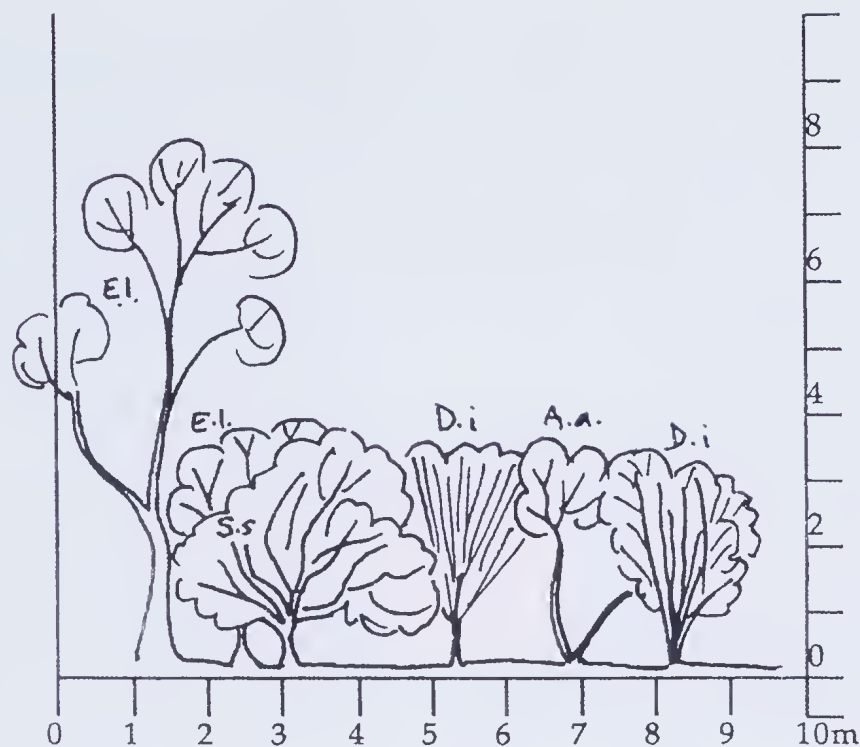


Figure 4. Profile (tree 10; ht 377 cm, stand of *Santalum spicatum* (S.s.) with *Eucalyptus loxophleba* (E.l.) with *A. acuminata* (A.a.) and *Dodonaea inaequifolia* (D.i.), at site RO).

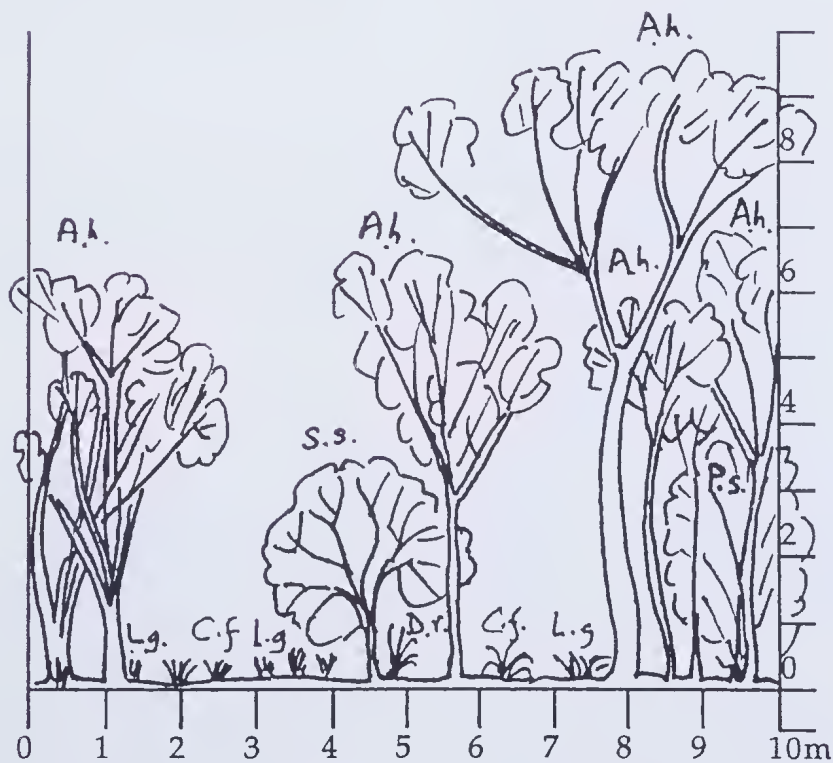


Figure 5. Profile (tree 24; ht 330 cm, stand of *Santalum spicatum* (S.s.) with *Allocasuarina huegeliana* (A.h.), *Chamaexeros fimbriata* (C.f.), *Dianella revoluta* (D.r.), *Lepidosperma drummondii* (L.d.), and *Persoonia striata* (P.s.) at site RE).

localities where more than two thirds of sandalwood have it nearby. The R locality has fewest *A. acuminata* with none at RS and RE. When *A. acuminata* is absent then *Dodonaea inaequifolia* and *Alyxia buxifolia* are present at PA and *Allocasuarina huegeliana* at CK3B. At RO, *D. inaequifolia* is also important (Fig 4); at RE *A. huegeliana* dominates (Fig 5); at RS and R both *Dodonaea viscosa* and *Leptospermum erubescens* are the main shrubs present. *Acacia colletioides*, *A. hemiteles* and *A. erinacea* are only important as associates of *S. spicatum* at PA, the woodland locality.

Not all species listed in Table 2 are likely to be valuable as host plants to sandalwood and the 8 species listed once only may be assumed to be chance co-occurrences. For example, *Eucalyptus crucis* is common at SRNR at rock edges but there is only one joint occurrence with sandalwood. Similarly 5 other species from locality R, including *Persoonia striata* (Fig 5), occur once with sandalwood. Some 27 species co-occur with sandalwood at a frequency of 5% or less. Sandalwood is more often found adjacent to many of these species rather than within patches of them. Thus, sandalwood does not occur under trees of *Eucalyptus capillosa*, that, similar to the related *E. wandoo* Blakely, tend to lack a shrub understorey (Lamont 1985). Many of the sandalwood with either *Eucalyptus loxophleba* or *E. capillosa* also have *Acacia acuminata* present. Relatively poor crowns of *A. acuminata* (e.g. CK3B) compared with the same species where *S. spicatum* is absent, suggest it is damaged by the parasite.

Of the thicket species, *Leptospermum erubescens* is highest up the list. Sandalwood does not occur within dense thickets of this species, rather to the edge. The thicket (or broom bush) habit of most *Melaleuca* species, and of *Allocasuarina campestris* and *Calothamnus asper* (important at CK3), may hinder the development of *S. spicatum* as it is not found directly under shade (Figs 4, 5).

Reproductive efficiency

Flowering has been observed regularly in March but the intensity of flowering on particular individuals does not seem to be related to the size of the following nut crop. In March 1994, 50 sandalwood trees at 3 localities were examined for freshly fallen nuts from the 1993 season. Thirty six trees (72%) had 174 ($\pm$ se 36) nuts and 14 had none. Of these 36, 14 of 27 examined in March 1995, (i.e. 52%), had 83 ($\pm$ se 36) nuts and 13 had none (9 were not examined). Thirty three of the same 36 trees were examined in March 1996 when 29 (88%) had 80 ($\pm$ se 18) nuts.

In March 1995, a total of 76 trees at 3 localities was examined for nuts from the 1994 season. Thirty seven (49%) had 56 ($\pm$ se 15) nuts and 39 had none. In March 1996, 139 trees from 4 localities were examined for nuts from the 1995 season. Ninety seven (70%) had 149 ($\pm$ se 36) nuts and 42 had none.

There are significant differences by locality for the 36 trees with fruit from the 1993 season ($F = 6.371$; $P = 0.005$). Those at CK3 had more nuts ($369 \pm$ se 101; $n = 9$) than at PA (mean $118 \pm$ se 36; $n = 14$) and R ($100 \pm$ se 36; $n = 13$). The latter two do not differ significantly. Differences are not significant for those of the 36 that also fruited in 1994; CK3, $82 \pm$ se 19 ($n = 2$); PA, $24 \pm$ se

12 ($n = 4$); R, $112 \pm$ se 61 ($n = 8$); or 1995; CK3, $105 \pm$ se 52 ($n = 6$); PA, $100 \pm$ se 34 ($n = 11$); R, $49 \pm$ se 17 ($n = 12$).

Mean nut numbers differ significantly by locality for the 76 examined in 1995 ($F = 4.137$; $P = 0.02$). Those at R have most ($68 \pm$ se 32; $n = 16$ of which 13 had nuts and 3 did not). The other 2 sets have significantly fewer nuts: CK3, $22 \pm$ se 7 ($n = 36$), of which 17 had nuts and 19 did not; PA, $9 \pm$ se 4 ($n = 24$), 7 with and 17 without nuts. Those with nuts ($\Sigma n = 37$) have 83 (R); 46 (CK3); and 31 (PA) with $\pm$ se of 38, 12 and 8 respectively. These means do not differ significantly ($F = 0.992$, $P = 0.381$).

Significantly more nuts ($F = 3.806$; $P = 0.012$; $\Sigma n = 139$) are again found for 1996 (from the 1995 fruit season) for R trees ($258 \pm$ se 110, $n = 29$, of which 28 had nuts), when trees are compared for each of the 4 localities. The trees from CK3B ($96 \pm$ se 38, $n = 34$, of which 31 had nuts), PA ($88 \pm$ se 21, $n = 32$, of which 28 had nuts), and CK3 ($20 \pm$ se 9, $n = 44$ of which 10 had nuts) do not differ in nut numbers. Those with nuts ($\Sigma n = 97$) have means of 267 (R); 106 (CK3B); 100 (PA); and 88 (CK3) with $\pm$ se of 113, 41, 23 and 31 respectively. These means do not differ significantly ($F = 1.461$, $P = 0.230$).

Numbers of nuts below trees from the 1995 crop are highly correlated with each of 1996 measures of mean crown diameter (CD), tree height (Ht) and stem diameters (SD 5, 15 or 130 cm). For example, of the 34 trees at CK3B correlation coefficients are as follows; SD at 130 cm, $r = 0.738$ ($P = 0.001$); CD, $r = 0.625$ ($P = 0.001$); Ht, $r = 0.597$ ($P = 0.01$); SD 5 cm, $r = 0.488$ ($P = 0.01$); and SD 15 cm, $r = 0.374$ ($P = 0.05$).

Division of CK3B trees into 2 sets based on height $>$ or < 300 cm shows that for 15 larger trees (> 300 cm tall, mean $383 \pm$ se 21 cm) the nut number per tree is 176 ($\pm$ se 81). Nuts are correlated with tree dimensions as follows; SD 130 cm, $r = 0.780$ ($P = 0.001$); Ht, $r = 0.698$ ($P =$

Table 3

Statistics for numbers of nuts counted on 10 trees of Locality R in each of 1994, 1995 and 1996.

SET	Tree	Tree height (cm) in 1996	Number of nuts counted in		
			1994	1995	1996
R	1	225	191	500	50
R	30	324	480	215	216
RS	16	158	28	3	18
RS	17	178	30	7	45
RS	18	161	8	2	20
RS	19	130	0	0	0
RE	25	273	172	19	33
RE	24	330	160	40	23
RE	22	311	42	111	15
RE	23	167	7	0	10
	Mean	226	112	90	43
	se	24	47	51	20
	F =	5.049	7.624	13.386	4.691
	P =	0.044	0.018	0.004	0.051
Means	R	275 ^a	336 ^a	358 ^a	133 ^a
	RS	157 ^b	17 ^b	3 ^b	21 ^b
	RE	270 ^a	95 ^b	43 ^b	20 ^b

superscript letters indicate significant differences within columns, by LSD test.

= 0.01); CD, $r = 0.674$ ($P = 0.01$); SD 5 cm, $r = 0.525$ ($P = 0.05$); but not SD 15 cm, $r = 0.284$ (NS). For the 19 smaller trees (<300 cm tall, $237 \pm \text{se } 11$ cm) the nut number per tree is $34 (\pm \text{se } 10)$ and nut numbers are correlated only with CD, $r = 0.732$ ($P = 0.001$). Other values are; Ht, $r = -0.034$ (NS); SD 15 cm, $r = 0.398$ (NS); SD 5 cm, $r = 0.164$ (NS); and SD 130 cm, $r = 0.029$ (NS).

At locality R, 1996 nut numbers vary from 1 to 2 500. Despite considerable variation, there is no significant difference in 1996 nut counts between the four sub-sets of R ($F = 1.653$; $P = 0.203$). The following summarises 1996 counts; set R, n with nuts = $8\,351 \pm \text{se } 308$, range 1–2 500; set RO, $n = 7$, $603 \pm \text{se } 259$, range 20–2 000; set RE, $n = 9$, $28 \pm \text{se } 9$, range 8–77; set RS, $n = 5$, $40 \pm \text{se } 11$, range 18–80.

Nut records are incomplete for the 3 year period but the available yields from 10 trees of locality R reveal significant differences between sets for each year (Table 3). RS trees are of smaller stature, yield fewest nuts, occur very close to rock (tree 19 is in a fissure) and have *Dodonaea viscosa* or *Lepidosperma* sedges as closest associates. Trees at R are taller, yield most nuts, occur in a range of distinctive habitats and of the two listed one is associated with *Acacia acuminata* and *Allocasuarina huegeliana*, the other with *Leptospermum erubescens* and *Dodonaea viscosa*. Trees at RE occur with *Allocasuarina huegeliana*, *Dodonaea viscosa* or *Leptospermum erubescens*. These 10 indicate a decline in nut production over the 3 seasons, although only 4 trees give largest yields for the 1993 fruit season and 3 have highest yields from the most recent season.

Consideration of the 1996 nut assessment ($n = 97$) suggests that quantity of nuts is extremely variable but the larger trees have more. The best fit of nuts with tree dimension is the exponential relationship;

$$\text{nuts} = 3.914 \times 10^{(0.00364 \text{ CD})}$$

($r^2 = 0.316$; Fig 6).

Seedlings

Sandalwood seedlings are present at each locality, with a mean stocking per ha of 39.8, excluding the diffuse set R (Table 1). Seedlings are not present with all trees e.g. on the rockier sites (R) no seedlings are present at either RE or RS. Seedlings are currently only found near or directly underneath putative parent trees. At

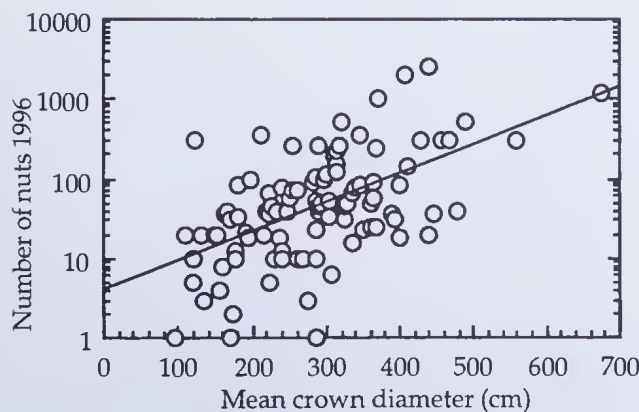


Figure 6. 1996 nut production and mean crown diameters.

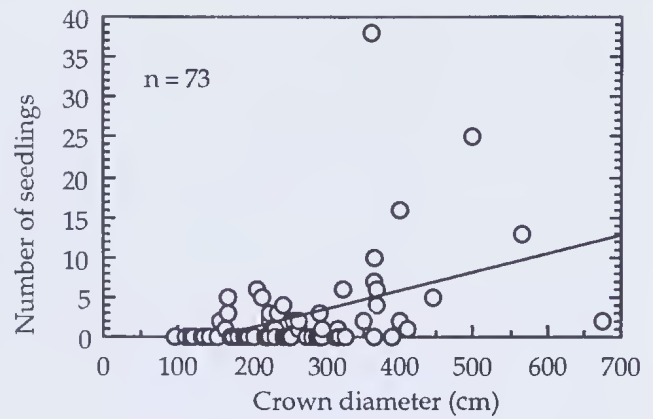


Figure 7. Relationship between seedling numbers and crown diameter of parent trees for $n = 73$ at localities PA and CK3B combined. Seedlings = $-3.539 + 0.02304$ Crown diameter (cm); $r^2 = 0.180$.

locality PA, 1996 seedling numbers near measured trees are correlated with the 1996 nut count ($n = 32$, $r = 0.805$, $P = 0.001$) and with soil depth ($r = 0.385$, $P = 0.05$). In contrast, at CK3B, seedlings are correlated with sandalwood height ($n = 34$, $r = 0.367$, $P = 0.05$) and SD 15 cm ($r = 0.398$, $P = 0.05$). Lumping PA and CK3B observations ($n = 73$) suggests that crown diameter is the best predictor of seedling numbers ($r = 0.424$, $P = 0.001$). Figure 7 illustrates the relationship described by the regression;

$$\text{seedlings} = -3.539 + 0.02304 \text{ crown diameter (cm)}$$

$r^2 = 0.180$ ($n = 73$, $P < 0.001$). If trees with no seedlings are excluded, then the regression is not significant;

$$\text{seedlings} = -0.9566 + 0.02164 \text{ crown diameter (cm)}$$

$r^2 = 0.111$ ($n = 31$, P is NS).

At CK3B, the 119 seedlings represent a mean of $3.5 (\pm \text{se } 1.2)$ per tree ($n = 34$). However, 12 trees have no seedlings, those 22 with seedlings have 1–38 present with $5.4 (\pm \text{se } 1.7)$. Sixteen sandalwoods have 1–5 seedlings each, accounting for 73% of all seedlings. The largest numbers per tree are associated with tree 26 (38 seedlings) and tree 11 (16 seedlings). Seedlings associated with the 15 tallest (> 300 cm) trees ($6.7 \pm \text{se } 2.5$ seedlings) are not significantly correlated with any other observations. Those associated with the 19 shorter (< 300 cm) trees are fewer in number ($0.9 \pm \text{se } 0.3$) and

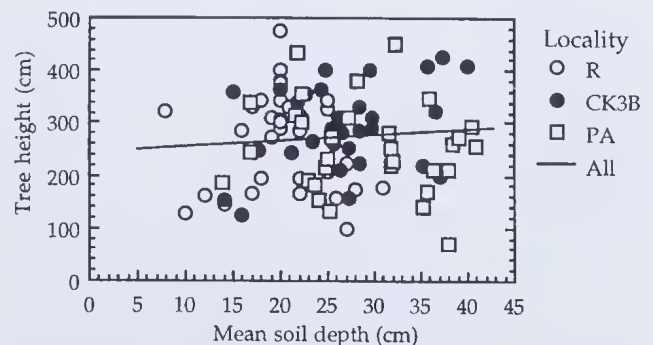


Figure 8. Relationship between tree height and mean soil depth for sandalwood trees.

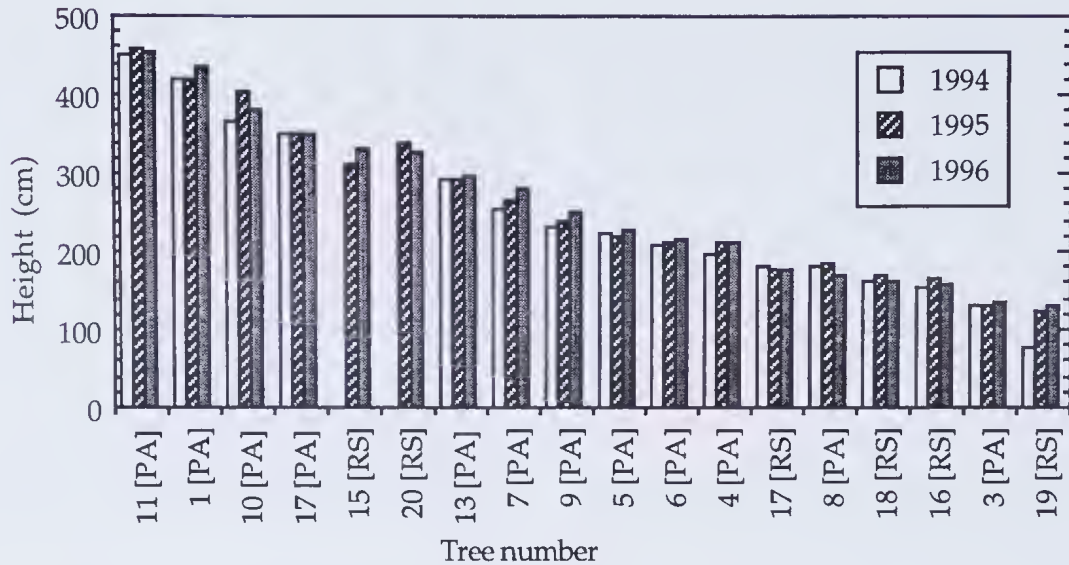


Figure 9. Measured heights for 18 trees 1994–1996 (Sites PA and RS).

only (negatively) correlated with SD 130 cm ($n = 11$, $r = -0.645$, $P = 0.05$).

Soil

Large sandalwoods with past high nut production have considerable litter debris beneath the crown. Observation suggests this facilitates growth of introduced annual grasses (*Briza*, *Avena*). Soils are generally sandy loams and mean soil depth taken near sandalwood trees differ significantly between 3 localities (CK3 not available; $F = 15.510$, $P = 0.001$). Soil is deepest at PA ($28.9 \text{ cm} \pm \text{se } 1.3$, $n = 32$), similar at CK3B ($27.0 \pm \text{se } 1.2$, $n = 32$) and significantly shallower at R ($20.6 \pm \text{se } 0.8$, $n = 36$). Mean soil depths at each of the R subsets are similar, between 19 and 21 cm.

Correlation analysis reveals that soil depth is significantly positively correlated with tree height for CK3B trees ($n = 32$, $r = 0.421$, $P = 0.05$). Soil depth is not significantly related to any other dimensions recorded. The linear fit for CK3B trees is;

$$\text{plant height (cm)} = 137 + 6.171 \text{ soil depth (cm)}$$

(1996, $n = 32$, $r^2 = 0.177$). Plant height is negatively

correlated with soil depth for plants immediately adjacent to granite, locality R;

$$\text{plant height (cm)} = 324 - 3.211 \text{ soil depth (cm)}$$

(1996, $n = 36$, $r^2 = 0.028$, P is NS). A similar, non-significant, relationship occurs with PA trees. When these 3 locality sets are combined (Fig 8) plant height has no correlation with soil depth.

The 15 taller trees ($> 300 \text{ cm}$) at CK3B have a soil depth of $28.6 (\pm \text{se } 1.9)$ compared with the 19 trees $< 300 \text{ cm}$ with $24.6 (\pm \text{se } 1.5)$. This difference is not significant.

Growth

Six of the 10 taller sandalwoods (Table 1) are in CK3B, which also has the tallest individual sandalwood. The upper limit to growth is likely to be determined by a combination of site influences and may require a considerable time period for it to be established. Tree architecture in parasitic tree species appears less robust and formalised than in free living species. In sandalwood, growth increments are difficult to detect as foliage is brittle and easily lost to wind, bird damage and fungal infections. This affects height

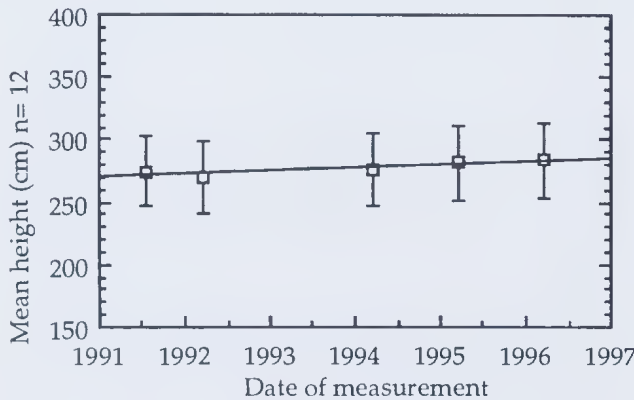


Figure 10. Mean heights and standard errors for 12 trees consistently measured at locality PA.

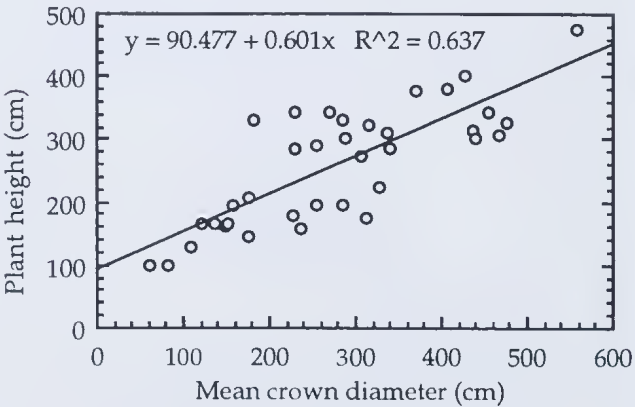


Figure 11. Relationship between plant height and crown diameter for plants immediately adjacent to granite (1996, $n = 36$).

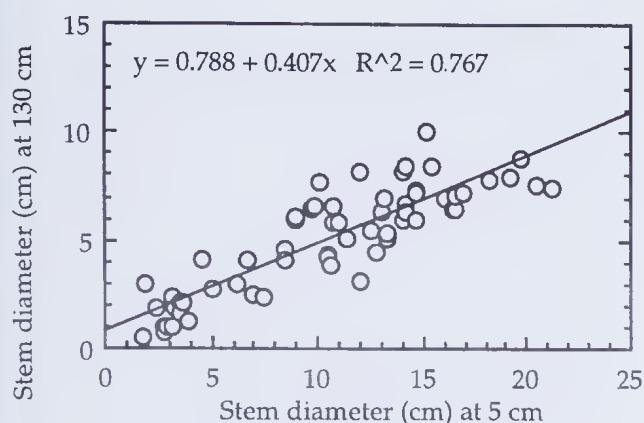


Figure 12. Relationship between stem diameters at 130 and 5 cm for measured trees at locality CK3 (two large outliers removed).

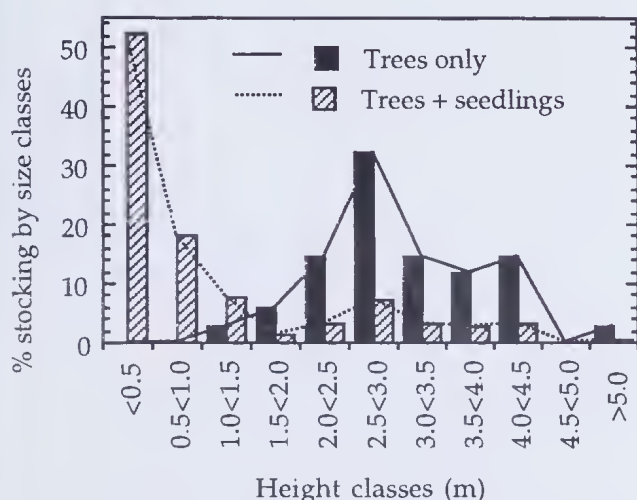


Figure 13. Sandalwood stocking March 1996 at CK3B, with and without seedlings.

and crown estimates. From year to year changes may be subtle (Fig 9) although seedling growth may be more easily recorded. For tree heights at least five years is necessary for reasonably robust estimates of change to be detected (Fig 10).

Tree architecture tends to be characteristic with some populations having a distinct main trunk, albeit not very long; others are shrubby with multiple branches from a metre or so. The characteristics of mature populations are revealed by correlations between dimensions. For example there is usually a consistent and reliable relationship between plant height and crown diameter (Fig 11) and between the several measures of stem diameter (e.g. Figure 12).

The problem of assessing population dynamics in relation to seedling establishment is important. Figure 13 indicates that seedling populations can be considered separately from that of trees or can be considered together with trees. Thus far, no seedling populations have been encountered away from mature trees.

Discussion

On granite exposures of the Darling scarp above Perth, the Christmas tree *Nuytsia floribunda* (Labill) R Br is common and may have a similar role in vegetation (Lange 1960) to that of the sandalwood described here. Sandalwood does not have the same ability to persist through suckering and populations may have greater genetic diversity than in *N. floribunda* or than *Santalum album* L which can sucker profusely. The phenomenon of clumping with individuals of seed origin may render populations more robust. However, some autoparasitism must occur amongst the several dense seedling clumps and this may reduce growth. Highest apparent densities are at localities adjacent to granite but areas sampled are comparatively small. Sandalwood clumping involves both large individuals and seedlings occurring in close proximity. Ultimately this results from poor seed dispersal. The large fruits appear not to be currently taken by emu (*Dromaius novaehollandiae* Latham) although evidence of its presence is seen frequently with scats heavily loaded with seed of *Eremophila ionantha*.

Continuous regeneration is suggested by seedling densities but is at present confined to clumps. R trees show greatest departure from a normal distribution with two peaks; this may have more to do with the variation in habitats encompassed than to past recruitment periods. Seedling presence near parent trees may reflect current rabbit pressure. It will be interesting to observe whether rabbit decline following the calicivirus virus coincides with sandalwood seedlings establishing further away from parent trees.

The distribution of sandalwood at SRNR reveals the circumstances in which it is able to persist. It is absent from pure stands of the larger eucalypt trees e.g. *Eucalyptus capillosa*, *E. salmonophloia* F Muell and *E. salubris* F Muell, presumably as these dominate their edaphic environments and may allow insufficient light for sandalwood. Competition for soil moisture in dry weather is the main factor limiting the stocking of large trees that can be supported in such stands. The taller woodlands are confined to areas of deeper soils with limited stands of salmon gum (*E. salmonophloia*) forming the tallest woodland stratum. Although sandalwood is absent with this species, *Santalum acuminatum* is able to occur (Keenan 1993). Sandalwood can persist in the vicinity of York gum mallee; this species is frequently in small patches that border *Acacia* and *Leptospermum erubescens* thickets.

Plant parasites can attack many hosts and can use multiple hosts simultaneously (Musselman & Mann 1978; Gibson & Watkinson 1989). A single *S. spicatum* may parasitise variable numbers and species of hosts (Herbert 1925). It is assumed that plants frequently with sandalwood are both good hosts and good survivors. Hosts that cause best parasite performance may suffer more from parasitism and there will be some upper limit to the amount of parasites that can be tolerated by particular host communities.

Whereas host preferences of epiphytic parasites can be observed directly, those of root parasitic trees can only be inferred without exploring root connections (Pennings & Callaway 1996). Pot trials with host/parasite pairs suggest direct negative effects on host

growth (Marvier 1996) and that growth is better when associated with some hosts rather than others (Rai 1990; Fox *et al.* 1996; Marvier 1996). Six of those listed are noted by Loneragan (1990) as host species; *Acacia acuminata*, *A. colletioides*, *A. hemiteles*, *Cassia nemophila*, *Eucalyptus loxophleba* and *E. capillosa*. The jam tree *Acacia acuminata*, the lily *Dianella revoluta*, the medium shrub *Dodonaea inaequifolia* and the tree *Allocasuarina huegeliana*, as the most frequent associates of *Santalum spicatum* at SRNR, are likely the best hosts. All except *D. inaequifolia* are present at the successful sandalwood plantation at Dryandra (Struthers *et al.* 1986) and Loneragan (1990) has indicated another *Dodonaea* (*D. lobulata* F Muell) as an important host. A species listed by Loneragan (1990) that does not feature in Table 2 is *Eremophila ionantha* (Diels) in Diels & E Pritzel. This is common at SRNR as an understorey species in eucalypt stands.

Species listed by Loneragan (1990) that are probably not important hosts with *S. spicatum* near granite areas at SRNR are; *Acacia colletioides* and *A. hemiteles*, and the eucalypts *E. loxophleba* and *E. capillosa*. These *Acacia* species, and *A. erinacea*, are associated with salmon gum (Fox *et al.* 1993) and only occur as associates of *S. spicatum* at PA, the woodland locality on slightly deeper soils. Other *Acacia* species of this reserve are confined to sandier soils where *S. spicatum* is entirely absent (e.g. *A. stereophylla*, *A. neurophylla* W Fitzg, *A. coolgardiensis* Maiden). Other evidence (Fox, unpublished) suggests that eucalypts generally are poor hosts and this is generally associated with competition for soil moisture (Lamont 1985). *Allocasuarina campestris*, *Melaleuca hamulosa* and *M. lateriflora* form thickets to < 3 m (Fox *et al.* 1993) and sandalwood does not occur amongst stands of these or of *Calothamnus asper*. Some overhead light appears necessary to support sandalwood growth. Loneragan (1990) listed *Casuarina cristata* Miq and *Dodonaea lobulata* F Muell, as hosts. These species are not found at SRNR but it is postulated that species in these genera (and *Allocasuarina*) are likely to be universally good hosts for sandalwood. The tree *Allocasuarina huegeliana* is of considerable interest as it provides the greatest standing biomass over much of the distribution of *S. spicatum* and, presumably, also the greatest volume of available roots for haustorial connections; *A. huegeliana* is often the dominant species of rockier areas. The frequency of occurrence of the perennial lily *Dianella revoluta* suggests that this species is probably utilised as a host by sandalwood. Earlier circumstantial evidence linking *D. revoluta* to sandalwood at Dryandra is alluded to by Struthers *et al.* (1986).

Low or sporadic fruit set is common in semi-parasites (Musselman & Mann 1978). Contrary to perceived belief (Loneragan 1990; Kealley 1991), sandalwood trees are regular in flowering. Flowering is more likely a photoperiodic response than one to rainfall, as buds invariably open at SRNR between February and May. The quantity of flowers, duration of flowering, fruit set and maturation are all variable and may depend on seasonal rainfall, prior fruiting history and tree size. Up to 700 flowers may result in only one fruit (Barrett 1987). Nut production is irregular (Davies 1976) and differs between trees and seasons. There is considerable range in yield with 2 000 to 2 500 nuts recorded from some larger trees. The proportion of trees fruiting in 1993 and

1995 is similar, and higher than in 1994. Similarly, the number of nuts per tree on those fruiting is lowest from the 1994 season. Of trees observed to have fruited in 1993 and also examined subsequently, mean nut production from the 1994 and 1995 seasons is about half that from 1993, and the lowest proportion of trees fruited again in 1994 compared with 1995. Significant differences in nut production between trees at different localities tend to be lost when trees barren in that year are not included in the analysis. However, it is of interest that trees at the more northern location produced most fruit per tree in the 1993 season whereas some trees from the rockier localities produced more nuts from both the 1994 and 1995 seasons.

Nut production from taller trees (> 300 cm height) is correlated with several dimensions of plant size, all reflecting age and relative maturity, but for smaller trees nut yield is only related significantly with crown diameter. This suggests that crown spread has more influence on nut yield than stem size or tree height.

Nut weight and diameter in *S. spicatum* differs in relation to longitude (Fox & Brand 1993), mainly associated with falling away of mean rainfall inland. Some trees located adjacent to granite may have higher effective soil moisture available in the fruit forming winter months due to redistribution. This may have an influence on the size of the nut crop. The massive loss of flowers (Barrett 1987), large nut size (Musselman & Mann 1978; Fox & Brand 1993), poor germination (Loneragan 1990) and brittle foliage suggests low resource efficiency is a physiological consequence of parasitism.

Regeneration of dominants is uncommon. Release from canopy held seed in eucalypts may compensate for irregular fruiting (Yates *et al.* 1994) but there is no such effect in sandalwood. The availability of viable seed may limit seedling regeneration and this is a topic for further research. Concern has been expressed that seedling regeneration of sandalwood is retarded by herbivore activity. Until 1996 rabbits and kangaroos were frequently seen at SRNR. A viral disease reduced kangaroo numbers in the summer of 1995–96, and rabbit numbers appear to fluctuate with myxoma virus outbreaks. It is possible that saturation of space under parents by nut material may have deterred rabbit herbivory. With the introduction of the calici virus it is possible that the next few years may see increased sandalwood regeneration, away from parent trees.

In the terminology used by other speakers at this symposium, some sites near granite outcrops may be termed as apron or petticoat places. These have shallow or poorly developed soils unable to support perennial species. Other sites lie in long narrow gaps between large rounded sections of granite where deeper or more developed soils do support perennials. Sandalwood is rarely found at such sites occupied by *Eucalyptus crucis*; these narrow garter sites lie at areas where the steeply shelving rock appears to dive beneath the regolith such that organic matter has accumulated and where soil moisture may be comparatively high. In supporting this long-lived eucalypt the sites may be too dry in summer to support sandalwood.

It is possible that sandalwood is restricted to relatively nutrient poor sites (Matthies 1995). Soils are sandy loams,

grey and gritty (Muir 1979). Both main tree hosts occur on granitic sandy soils (Lange 1960). However, granitic soils of the region are characteristically high in potassium (McArthur 1991), important in sandalwood nutrition (Struthers *et al.* 1986). The two important host tree species both fix nitrogen; *A. acuminata* (Roughley 1987), *A. huegeliana* (Rodríguez-Barrueco 1968). Best occurrence is often between or adjacent to different vegetation types. Such locations may provide the widest range of hosts (Kealley 1991) as sandalwood root extension is considerable and allow some access to better soils. Sandalwood is not found in very shallow soils but is also scarce in well-developed eucalypt woodlands where soil depth may be much deeper. Light competition coupled with root saturation may restrict it in such areas. Alternatively, present absence may result from lack of regeneration following exploitation last century.

The balance between competitive and host effects is related to growth conditions (Watkinson & Gibson 1988). Do larger parasites directly diminish host growth? *Acacia acuminata* is in poor condition near a number of sandalwood occurrences. Another favoured species, *A. tetragonophylla* (Loneragan 1990) is present, but now scarce, at location PA and may have declined due to sandalwood parasitism. Do host species differ in tolerance of parasitism? *Allocasuarina huegeliana* appears to be more robust than the *Acacia* species, it reaches a large size and probably persists longer. It may not suffer as much from parasitism as *A. acuminata*.

Conclusions

Hosts function as sources of water and nutrients for the parasite. Potential hosts may offer competition by reducing light available to the parasite. *Santalum spicatum* appears better able to occur adjacent to the lighter shade cast by the nitrogen-fixing host trees *Acacia acuminata* and *Allocasuarina huegeliana* than under most eucalypt species. Poor crown condition of *A. acuminata* near *S. spicatum* indicates that the parasite damages at least this host. It is considered that the particular edaphic environments that permit the development of the recognised host tree species of *Acacia acuminata* and *Allocasuarina huegeliana* to flourish are mainly responsible for the prolific occurrence of *Santalum spicatum* at Sandford Rocks Nature Reserve. It is possible that most species of *Dodonaea* are likely hosts for sandalwood.

The commercial size for harvest of sandalwood is a trunk diameter of > 127 mm measured at 150 mm from ground level (Kealley 1991). A number of trees in the populations at SRNR exceed this criterion.

Evidence is presented to demonstrate that there is no shortage of seedlings of *Santalum spicatum* in an environment where rabbits have been abundant. At the seedling stage sandalwood is shade tolerant but no mature trees occur under overhead shade. Four growth stages are postulated from the evidence produced;

- 1) initial establishment of small seedlings (1–2 years from seed);
- 2) persistence as seedling-sapling to ca 1 m height (2–8 years);
- 3) growth to mature size 2.5–3.5 m (10–30 years);

- 4) continued growth in stem diameter and crown spread, little change in height (30–100 years).

Acknowledgements: Thanks are expressed to my colleagues D R Barrett, A I Doronila and P M Reeve for assistance. Final year students of Terrestrial Ecology 301 have assisted with ecological studies at Sandford Rocks Nature Reserve. D Barrett, A Dick, D Ginger and S Collins are especially mentioned for measurements of the sandalwood trees in March 1996. The Department of Conservation and Land Management is acknowledged for permission to undertake research at Sandford Rocks Nature Reserve.

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Rocks as museums of evolutionary processes

J D Bussell & S H James

Department of Botany, The University of Western Australia, Nedlands WA 6907
email: jbusell@cylrene.uwa.edu.au

Abstract

The isolated granitic outcrops of Western Australia may harbour relics of the past such as *Isoetes* and *Stylidium merrallii*. They may also preserve a record of evolutionary change both within single populations and across population systems. Thus, the initial stages in the evolution of the complex hybrid genetic system are preserved amongst the extant lineages of *Isotoma petraea* on Pigeon Rock in the southwest of Western Australia. The elaboration of this bizarre genetic system is preserved across neighbouring outcrops. Study of *I. petraea* focuses attention on the evolutionary consequences of the controversial association of high levels of inbreeding with polymorphism for lethal genes within populations. In addition, it has generated novel and important insights into the genetic structure of Western Australian plant species and of evolutionary processes generally. Pigeon Rock and its unique living evolutionary museum is worthy of World Heritage listing, and should be preserved by removing the present stockyards and excluding the rock from the surrounding pastoral lease.

Introduction

Granite rock outcrops may be regarded as evolutionary museums on a number of fronts. They may house relict flora, such as the primitive *Stylidium merrallii* (Kenneally & Lowrie 1994), *Isoetes*, an ancient gymnosperm, and relict fauna. Alternatively, they may provide windows on evolutionary processes. The species supported by the granite outcrop habitat necessarily exist in an archipelago of small populations. These populations have a genetic structure which is a consequence of the levels of communication (or gene flow) between them, and of the devices they have evolved to cope. This paper deals with the sequential consequences of isolation and inbreeding imposed on *Isotoma petraea* (Lobeliaceae) on these granite rocks by the species' habitat preference and evolved adaptations. It traces the evolution of the genetic system, from a conventional outbreeding state with normal chromosome behaviour and high levels of seed production, to complex hybridity with self fertilisation, highly restricted chromosome behaviour and stringent seed selection systems.

Classically, diploid sexual reproduction is thought to promote evolutionary capability by enhancing the level of genotypic diversity among gametes through recombination at meiosis and the distribution of that diversity between lineages by biparental reproduction (Fisher 1930; Müller 1932). In contrast, sex, comprising meiosis and fertilisation, is now widely recognised as having a more primitive role. Firstly, corruptions of the DNA molecule which escape biochemical correction through cellular DNA repair mechanisms may be corrected by recombinational processes, even in somatic cells (Bernstein *et al.* 1988). Secondly, mutations arising from errors in the repair processes or from mobile genetic element activity, and which have become incorporated into the genome, may be removed from

lineages by outcrossing and segregation (Bell 1988). While mutation is the ultimate source of the variation which is exploited in evolution, most mutations are deleterious, ranging from selectively neutral to lethal. Modern interpretations also suggest that diploidy has evolved as a redundancy (fail-safe) mechanism for protecting the soma against mutational corruption (Maynard Smith 1988). Providing it operates within an allelically diverse gene pool, sexual reproduction can also raise evolutionary capability to new levels relative to those achievable by mutation alone, and diploid gene pools are more capable than those associated with haploidy. Evolutionary capability is thus a consequence of unencumbered sexual genetic repair. If the sexual system is encumbered with devices which diminish its efficiency, both the evolutionary capability of the lineage and its ability to remove deleterious mutations are impaired.

Classical population genetic theory predicts that gene flow between populations comprising a species' metapopulation will bind it into a single evolutionary entity. Breakdown of this communication, by geographic isolation or by inbreeding, will lead to divergence of the non-communicating populations and, perhaps, speciation. Classical theory predicts that population divergence will be accelerated under conditions of inbreeding, leading to the fixation of alleles, including deleterious recessives, through genetic drift. It also indicates that genetic diversity can be maintained in diploid gene pools only when the heterozygote is the most fit genotype. This condition is readily achieved by associative overdominance in which loci may be rendered stably polymorphic by linkage to deleterious recessives (Zouros 1994), even in inbreeding populations. Thus, the occurrence of deleterious recessives, which may occur in large numbers and are often measurable in terms of lethal equivalents, may provide diploid sexuality, including inbreeding populations, with evolutionary advantage. However, these lethal equivalents result in a genetic load.

The expression of the genetic load in a diploid sexual

population will depend on the breeding system. In a normally outbreeding population, deleterious mutations are expected to be effectively invisible, being masked by the uncorrupted DNA of the homologous chromosome (diploid redundancy). Outbreeding populations are thus predicted to accumulate elevated levels of heterozygosity for deleterious mutations. If the population is forced to inbreed, this genetic load will be expressed as inbreeding depression due to the formation of elevated levels of deleterious recessive homozygotes. In a normally inbreeding population, on the other hand, mutations should be regularly exposed as homozygotes and purged out of the gene pool if they are sufficiently deleterious (Lande & Schemske 1985; Charlesworth *et al.* 1990). Thus inbreeders may be expected to be relatively free of seriously deleterious recessives, and exhibit little inbreeding depression and a reduced genetic load. Empirical evidence (Husband & Schemske 1996) suggests that in outbreeding plants, higher levels of inbreeding depression are exhibited at earlier stages in the life cycle, especially at seed formation, whereas with inbreeders, inbreeding depression is more likely to be expressed at later stages in the life cycle, if at all.

Genetic system evolution in *I. petraea* contradicts many classical expectations, particularly in its maintenance of high genetic loads in self-fertilising lineages. This paper reviews the genetic phenomena in *I. petraea* which led to this situation and documents the evolution, in response, of complex hybridity, a genetic system which effectively maintains genetic hybridity in highly inbred lineages. In addition, alterations to phenotypic characters, their patterns of variance within the population system, and their association with genetic system adaptations are discussed. Finally, the relevance of the observations made on *I. petraea* to patterns of variation in other native plant species is briefly reviewed.

Inbreeding in *I. petraea*

I. petraea occurs in discrete isolated populations on granitic and other rocky outcrops of arid Australia. Due to this habitat preference, population size is often limited and subject to numerical fluctuation and genetic bottlenecks. These features alone would impose a measure of inbreeding upon the populations. In addition, populations may be characterised by different breeding systems. The primitive breeding system in *I. petraea*, and the Lobeliaceae generally, is one promoting outbreeding. Outcrossing may result when the stigma protrudes through the anther tube, dispensing the flower's pollen on the way, and then becomes receptive to pollen from other flowers.

Self pollination, or autogamy, results when the style fails to elongate and the stigma remains enclosed within the anther tube, receiving pollen from the same flower (James 1965). The frequency of stigma protrusion may be taken as a measure of outcrossing potential. Because of population size, habitat preference and the possibility of pollination between flowers on the same plant, populations exhibiting high frequencies of stigma protrusion may still be relatively inbred. In populations where little or no stigma protrusion occurs, inbreeding approaches 100 per cent. Thus, all *I. petraea* populations

are inbreeding to some extent, but some are much more inbreeding than others. The adoption of autogamy may be regarded as a means of reproductive assurance, and would be selected for where ovules would otherwise remain unfertilised (Jarne & Charlesworth 1993). In accordance with classical theory, inbreeding in *I. petraea* promotes genetic uniformity within and differentiation between populations.

I. petraea Population Differentiation

I. petraea populations differ with respect to their stigma protrusion frequencies (Table 1). While stigma protrusion frequencies show some variation according to environmental conditions, the population differences are largely retained whether the plants are grown in the glasshouse, garden or in their natural habitat. This demonstrates that the stigma protrusion frequency is genetically determined, to a large extent, and that the populations are genetically differentiated with respect to this character.

Population divergence is also evidenced in flower colour and a number of metric characters such as leaf and flower dimensions, and the number of ovules per flower. Flower colour may vary from white, through varying shades of patterned pink to deep purple and blue. There is considerable variation between populations, and little within, so that populations are generally characterised by a single flower colour.

Partitioning of variance in leaf, pedicel and flower dimensions into within plant, within population and between population components was performed (James 1978; SH James, *unpublished data*). The characters measured were not closely related to aspects of plant fitness. The analysis (Fig 1; only structural homozygotes considered at this stage) showed that for these characters, while comparable variance components were found at all levels as would be predicted by classical genetics for

Table 1

Proportion of stigma emergence of plants from various populations of *Isotoma petraea*. Field measurements are given where possible. For plants from the same population, stigma emergence is usually higher in the more mesic garden and glasshouse environments than in the field. Measurements of stigma emergence other than those from the field will generally be an overestimate.

Population	Genetic System	Stigma emergence	Where Measured
Rainy Rocks	7II	1%	Field
Pigeon Rock	7II/⊙6	2%	Field
Iron Knob	7II	6%	Field
Victoria Rock	7II	32%	Garden
Merredin Peak	⊙14	40%	Garden
Boorabbin	7II	42%	Glasshouse
3 Mile Rock	7II/⊙10	56%	Garden
Moorine Rock	⊙12	79%	Garden
Bullabulling	7II	91%	Garden
Gnaribine Rock	7II	100%	Garden
Yacka Rock	7II	100%	Field
Disaster Rock	7II	100%	Field

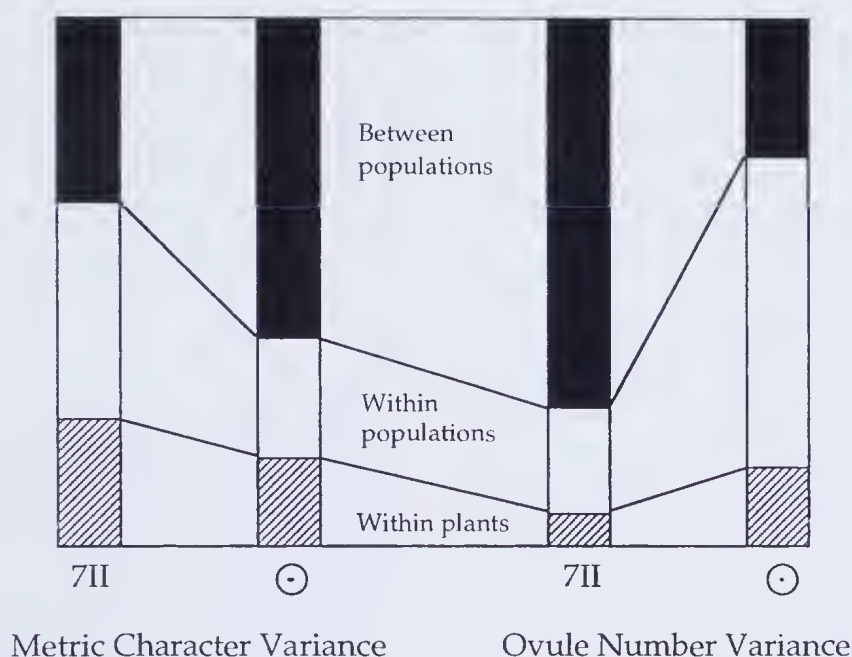


Figure 1. Partitioning of components of total variance for structural homozygote (7II) and complex hybrid (⊙) populations of *Isotoma petraea*. The distribution of variance reflects genetic system and selective importance of the characters (see text).

interbreeding populations, the greatest variance component was within populations. However, partitioning of variance for the average number of ovules per ovary (Kiew 1969) contrasted with that for the metric characters in that there was little variance within plants and by far the largest component was found at the between population level (Fig 1). This may be explained in that the number ovules produced may be expected to be a significant component of fitness and that it should be rigorously selected within populations. These observations generally conform with the expectation of differentiation between isolated populations.

Inbreeding, the Distribution of Deleterious Alleles and the Accumulation of Lethals

Half of the gametes produced by an organism heterozygous for a deleterious mutation will be free of the defective allele. On selfing, one quarter of the progeny will be homozygous for the mutation, one half heterozygous, and one quarter free of the mutation. Thus, sexual reproduction allows a self-fertilising heterozygote to remove deleterious alleles. However, providing the deleterious homozygote is only slightly inferior to the heterozygote and the other homozygote, it may persist in the population (Charlesworth *et al.* 1990). With stochastic effects associated with small population size and bottlenecks, the deleterious allele may actually become fixed in the population. It then cannot be removed without genetic communication from another population. Further deleterious mutations may similarly become fixed leading to the accumulation of debilitating mutations by a process analogous to Müller's ratchet (Müller 1964; Lynch & Gabriel 1990).

In addition, if both of a pair of homologous chromosomes carry deleterious alleles, mutation-free

gametes can only be produced by a recombination event occurring between the two heterozygous loci at meiosis. In *I. petraea*, recombination processes, which result in chiasma formation at meiosis, are strongly localised to the ends of the chromosomes. This means that recessive deleterious alleles occurring in pairs in the body of each chromosome cannot be removed in a strictly self-fertilising lineage and will accumulate (James *et al.* 1990; James 1992). Normally in *I. petraea* there are 7 pairs of homologous chromosomes which form seven bivalents (7II) at meiosis. Each pair of homologous chromosomes is thus effectively a single supergenic locus with the two homologues being the two alleles (James *et al.* 1990; James 1992), each loaded with deleterious, even recessive lethal, mutations.

For each supergenic locus, 50% of the selfed products will be heterozygous and 50% homozygous, so for 7 such loci only $1/2^7$ of the progeny will display parental levels of heterozygosity. The genetic load, that is, the proportion of inviable or inferior progeny of varying degrees of homozygosity for deleterious mutations, will approach 127/128 as the deleterious mutation content of each supergenic allele approaches lethality. This load strongly diminishes the reproductive potential of inbreeding populations, a problem which generates a focus for natural selection and adaptive evolution.

On the other hand, outbreeding populations handle their deleterious mutations much more effectively. Outcrossing facilitates the removal of deleterious alleles, even with chromosomes that show chiasma localisation. The lower frequency of homozygotes in outcrossing lineages, especially for newly mutated alleles, impedes any ratchet driven accumulation of deleterious alleles. The potential for genetic debilitation in populations with significant levels of cross pollination is therefore much lower or negligible, compared to that of strict inbreeders.

Competitive Ability of 7II Material of Contrasting Levels of Hybridity

The debilitating effects of inbreeding in *I. petraea* have been demonstrated in several unpublished dissertations (Cohen 1982; Playford 1987; SH James & N Cohen unpublished data). Cohen (1982) compared the performance in competition experiments of selfed and outcrossed progenies from populations characterised by different levels of inbreeding. Pairwise competition trials were established by sowing, intermixed into pots, two progeny arrays of different origins (Table 2). Progeny arrays were derived from 7II selfs, 7II intrapopulational crosses, 7II interpopulational crosses and selfed complex hybrids (see below). Within pots there were generally a few clearly superior plants and a number of suppressed weaklings, and replicate pots were consistent. Almost all comparisons were highly determinate in their outcomes, with the superior genotype clearly apparent from both aerial biomass (Table 2) and number of plants. Where indeterminate results occurred, they were most likely in competitions involving progenies of the same hybridity class, and especially where interpopulational hybrids were involved. The mean competitive index calculable from the results may be viewed as a measure of the relative vigour of each progeny type.

The most effective competitors were the progeny of crosses within 7II populations, and by far the poorest

Table 2

Mean competitive index of progenies of differing hybridity classes, listed in decreasing order of competitive ability (see footnote).

Hybridity Class	Progeny Array	Mean Competitive Index
7II Intrapop Cross	7II Gnarlbine Rock	0.91
7II Self	7II Gnarlbine Rock	0.77
7II Intrapop Cross	7II Victoria Rock	0.82
7II Intrapop Cross	7II Boorabbin Rock	0.76
Complex Hybrid Self	The Humps	0.55
Complex Hybrid Self	Mt. Stirling	0.56
Complex Hybrid Self	Keokanie Rock	0.54
7II Interpop Cross	Victoria Rock x Boorabbin Rock	0.46
7II Interpop Cross	Yellowdine x Wargangering Rock	0.35
7II Interpop Cross	Victoria Rock x Mt. Caudan	0.11
7II Self	Boorabbin Rock	0.09
7II Self	Victoria Rock	0.01

Twenty five seeds of each of 2 progeny arrays of contrasting hybridity levels were sown intermixed and directly into a 125 mm pot containing a standard potting mix. Seeds had previously been tested to ensure uniform germination rates. All plants greater than 20 mm in height were then harvested at the soil surface after 6–8 months of free competition, counted, weighed and identified using GOT, LAP, PGM or IDH assays (James *et al.* 1983). This process was performed in triplicate for each pair of contesting progenies for 3 progeny arrays at each of 4 hybridity levels in all pairwise comparisons (198 pots). At harvest the relative aerial biomass of each competing type in each pot was calculated as a decimal fraction and averaged for each group of three replicates. The mean competitive index for each progeny type was calculated as the average of the aerial biomass decimals for all competitions involving the progeny array, but excluding within hybrid level comparisons. A similar index was calculated for relative numbers of plants; results closely mirrored those for aerial biomass and are not presented here.

were selfed progeny of the 7II plants (Table 2). An exception was the selfed 7II Gnarlbine Rock progeny, which was rated third best of all the progenies. These findings may be related to the degree of outbreeding in the source populations as indicated by their stigma protrusion frequencies. Both the Victoria Rock and Boorabbin populations have a reduced incidence of stigma protrusion (Table 1). These populations are composed of highly inbred lineages, each carrying their own suite of accumulated deleterious recessives, many of them in homozygous condition. Intrapopulational crosses will have many of these deleterious recessives masked in heterozygosity and thus display considerable heterosis over selfs. Gnarlbine Rock plants are much more outcrossed (Table 1), so that the lineages within this population may be expected to have accumulated fewer deleterious recessives. It is no surprise that self progeny from this population performed as well as intrapopulational crosses from other populations. They were, however, inferior to Gnarlbine Rock intrapopulational crosses, in keeping with expectations. The superiority in all cases (including Gnarlbine) of intrapopulational hybrid seedlings over selfed seed from the same population strongly suggests that competition amongst seedlings in natural seed beds would ensure the survival of only the most heterozygous types.

Intropopulational crosses were somewhat unpredictable and exhibited competitive abilities generally inferior to 7II intrapopulational crosses, but superior to 7II selfs (apart from the Gnarlbine Rock selfs; Table 2). Different arrays of deleterious mutations would have accumulated in the various genetically diverged and reproductively isolated 7II populations, so that crosses between them would be expected to result in heterotic hybrids. However, the unpredictable performance of the interpopulational cross progenies as compared to the deterministic performance of other hybridity classes indicates that these hybrids combine non-coadapted genomes, are somewhat unstable, and may be expected to exhibit less than optimal performance.

These results mirror previous work in which varying degrees of heterosis were generated in progeny of artificial interpopulational *I. petraea* hybrids (Beltran & James 1974). Dry weights of parental, F1 and F2 material, grown without competition under constant experimental conditions were compared. In all cases, the F1 yielded greater dry weight than the mid-parental value, and generally exhibited considerable heterosis over the poorer performing parent. In some cases the F1 performed better than both parents. These results conform to expectations when viewed in terms of stigma protrusion. The poorest performing parents (Iron Knob, Rainy Rock) had very low stigma protrusion frequencies (Table 1) and were highly inbred, so it was not surprising that F1s performed much better than the selfs of these parents. The most outbred populations in the study (Yackackine ["495"] and Disaster Rock) generally did not exhibit heterosis for dry weight accumulation when crossed to plants from other populations.

We conclude that inbreeding populations of 7II *I. petraea* are somewhat debilitated by the accumulation and fixation of deleterious recessive mutations and they show significant levels of heterosis following both inter-

and intrapopulation crossing. Inbreeding does not purge the deleterious recessives from the gene pool. In addition, a higher level of outbreeding in 7II *I. petraea* populations leads to the incorporation of only low levels of recessive lethals into the gene pool, a minimum genetic load and little, though definite, inbreeding depression. These conclusions refine the generally accepted relationships between the breeding system, genetic load and inbreeding depression and are best understood in terms of the role of sexuality in genetic repair or cleansing.

The Pigeon Rock Population

The Pigeon Rock population is a very significant one in the evolution of *I. petraea* since it is in this population that complex hybridity evolved. Complex hybridity combines autogamy, a balanced lethal system and permanent hybridity for complexes generated by chromosomal interchanges (reciprocal translocations) (Darlington 1958; James 1965; Carson 1967; Holsinger & Ellstrand 1984). Pigeon Rock is composed of plants fitting two broad genetic types, with a number of lineages in each. Ancestral structural homozygote (7II) and derived complex hybrids co-exist in stable proportions of about 1:2 respectively (James *et al.* 1990).

Models for the evolution of the genetic system (James *et al.* 1990; James *et al.* 1991) propose that *I. petraea* on Pigeon Rock was initially 7II with an acquired autogamous habit (Table 1). This meant the population comprised essentially genetically isolated lineages, predisposed to the accumulation of deleterious mutations. The genetic load approached 127/128 as outlined above, with each supergenic allele carrying a lethal equivalent. In this genetic environment seed aborting lethals were generated, in the form of duplications and deficiencies, by chromosome segment

transposition, probably mediated by transposable elements. Abortion of seed due to these deficiencies had the benefit of reducing allocation of maternal resources into incompetent, homozygous seeds.

In Pigeon Rock complex hybrids, the initial seven supergenic loci have been reduced to five by coalescence of three of the bivalents into a single supergenic locus. During meiosis there are 4 bivalents plus a ring of six ($\odot 6$) visible at metaphase 1. The $\odot 6$ consists of 2 complexes, N and S, each of whose 3 chromosomes are placed alternately in the $\odot 6$, and held in place by chiasmata at their homologous ends. The duplications described above facilitated the origin of complex generating interchanges by enabling recombination between homologous segments in otherwise non-homologous chromosomes (James 1970; James *et al.* 1991).

Each $\odot 6$ plant is an NS heterozygote which produces only N and S gametes. Gamete viability depends on regular segregation of the N and S chromosomes to opposite poles at anaphase-1 of meiosis. NN homozygotes are avoided since the N complex is not transmissible in pollen. SS homozygotes are eliminated by seed abortion, elaborated from the seed abortion system which existed prior to complex hybridity (James *et al.* 1991). The NS $\odot 6$ complex hybrid is superior to the 7II structural homozygote in that it potentially represents a 4-fold increase in the number of fully heterozygous progeny ($1/2^5$ compared to $1/2^7$). The genetic load is thus reduced to 31/32.

The proposed model for the evolution of complex hybridity is supported by a number of lines of evidence. Firstly, mathematical models suggest that, given the constraints seen at Pigeon Rock, complex hybridity will rise to the level of prominence seen there (James *et al.* 1990). Secondly, allozyme marker heterozygosity, which would also act as a marker for deleterious mutation

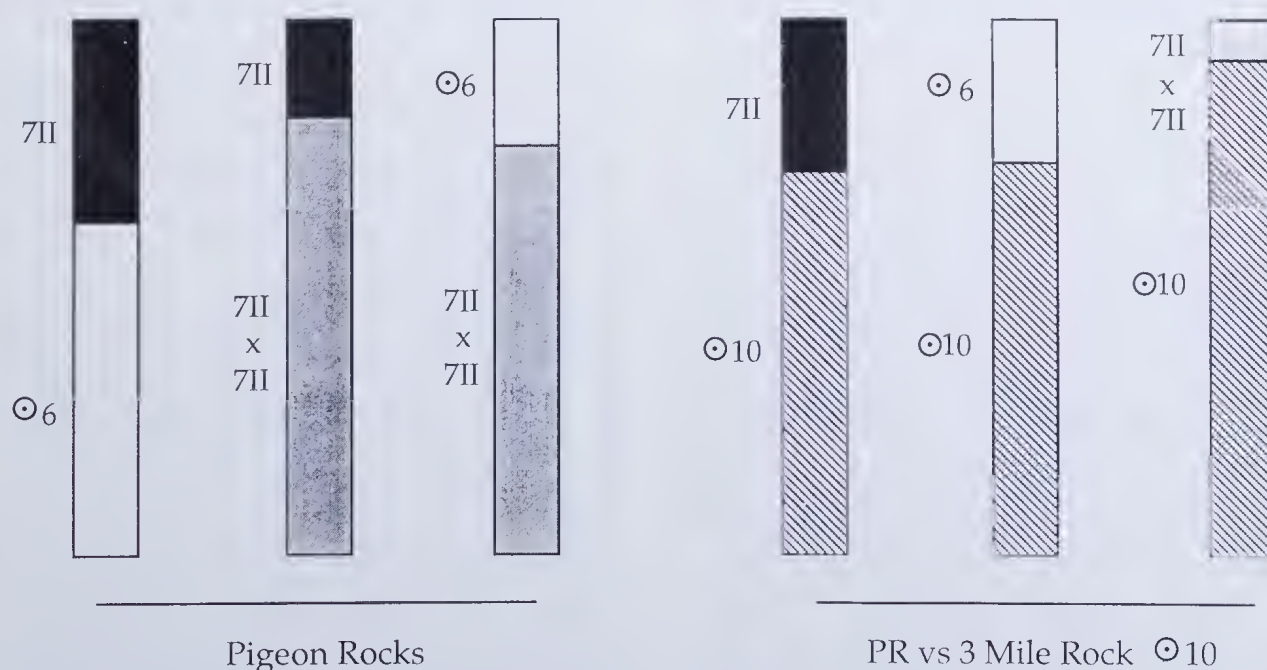


Figure 2. Competition experiments involving Pigeon Rocks selfed 7II, intrapopulation 7II x 7II crossed, selfed 7II and selfed 3 Mile Rock 10 progenies. Methods similar to those described in Table 2.

heterozygosity, is noticeably greater in the $\odot 6$ than the 7II (James *et al.* 1983). Thirdly, a series of competition experiments (Playford 1987) similar to those described above showed that the various levels of hybridity at Pigeon Rock were rated as might be expected from Table 2. Selfed 7II material from Pigeon Rock performed extremely poorly when pitted against its intrapopulation 7II x 7II rivals (Fig 2). The selfed 7II was inferior almost to the same extent against the selfed $\odot 6$ (Fig 2), a finding of obvious importance for the establishment and maintenance of the genetic system at Pigeon Rock. 7II x 7II crosses were superior to the $\odot 6$, but these would occur only very rarely, if at all, in the natural population and would not appreciably affect the 7II: $\odot 6$ balance. Finally, preliminary results of a molecular phylogeny using Random Amplified Polymorphic DNA strongly support the hypothesis that the $\odot 6$ originated from a Pigeon Rock 7II lineage exhibiting elevated seed abortion.

Resolution of the mechanism of evolution of complex hybridity on Pigeon Rock is particularly instructive. It demonstrates circumstances in which recessive lethal genes which operate early in seed development may accumulate in inbred lineages, a somewhat unexpected and controversial phenomenon (*cf* Husband & Schemske 1996).

Elaboration of Larger Ringed Complex Hybrids

There are many populations of complex hybrid *I. petraea*, all extending in a south-westerly direction from Pigeon Rock (James 1965; James 1970). It is thought that a series of migrations occurred, starting with the Pigeon Rock $\odot 6$. Hybridisation of an immigrant $\odot 6$ complex hybrid from Pigeon Rock with plants of the invaded 7II population would generate heterotic hybrids which were also heterozygous for numerous duplications and deficiencies arising from the seed abortion systems in the Pigeon Rock parent. The duplications facilitated further interchanges and allowed the coalescence of the genome into fewer supergenic loci, while the deficiencies formed the basis of a new balanced lethal system. Thus, interpopulation hybridisation involving the Pigeon Rock $\odot 6$ complex hybrid was able to generate new complex hybrids with larger rings in the recipient population. Migration of the new, larger ringed complex hybrid to the next 7II population led to further elaboration of the complexes so that the number of chromosomes incorporated into the ring progressively increased, in general, the further from Pigeon Rock. Usually each population is characterised by a single meiotic configuration and a very restricted array of genotypes (James 1970; James *et al.* 1983), indicating that a single, most fit complex hybrid type has displaced all others. Complex hybrid populations at the extreme of the genetic system's range are $\odot 14$. The $\odot 14$ s have a single supergenic locus and a genetic load reduced to 1/2.

Competition experiments have again demonstrated the feasibility of this model. Complex hybrids performed somewhat better than interpopulation 7II x 7II crosses, and markedly better than 7II selfs (Table 2). The 3 Mile Rocks $\odot 10$ out competed both 7II and $\odot 6$ material from Pigeon Rock (Fig 2) indicating that, at least in this case,

the larger ring confers more vigour than the smaller one. The $\odot 10$ was also victorious over Pigeon Rock 7II intrapopulation crosses (Table 2), which was perhaps not according to expectations, but which might be explained on the grounds of a generally high level of relatedness and genetic debilitation among the Pigeon Rock 7IIs.

Complex hybridity is a highly specialised system and very stable once established in a population. Crosses between plants from different complex hybrid populations display negative heterosis in the F1 (Beltran & James 1974), suggesting that a level of hybrid vigour or heterosis at least equivalent to that exhibited by 7II x 7II interpopulation crosses (see Table 2) is already conserved within plants. In addition, it may be expected that the two complexes associated in a naturally occurring complex hybrid are highly selected for mutual co-adaptation whereas complexes from different populations, which have not been mutually selected, are not coadapted and perform less well together.

The selective advantage of complex hybridity has been explained, in the past, in terms of a "pursuit of hybridity" (Darlington 1939; James 1965; Carson 1967). Detailed study of the genetic properties and competitive abilities of natural populations of *I. petraea* distributed over the granite rocks of Western Australia has led to identification of the masking of deleterious mutations as the underlying basis of hybrid superiority and to a detailed appreciation of the pathways followed in this evolutionary pursuit. CD Darlington's concept of the "pursuit of hybridity" in evolutionary progress has always been controversial, but we can be certain that it is a real and powerful phenomenon.

Adaptive Responses of Complex Hybrids

The pursuit of hybridity in highly inbreeding populations of *I. petraea* has led to the evolution of complex hybridity. In this genetic system, the seven pairs of chromosomes have been coalesced to form two complexes which are mutually coadapted alleles of a single supergene. These complexes are distributed from parent to offspring without change, for there is essentially no recombination within their chromosomal components, and their components cannot assort independently as is possible in the primitive seven bivalent forming types. Thus, recombinational capability, which is often taken to be the primary value of sexual reproduction in normal diploid sexual species, and the source of evolutionary capability, is highly suppressed in these derived complex hybrids. However, the complex hybrids exhibit quite striking evolutionary adaptations in important components of their reproductive biology (summarised in Table 3).

First, the complexes for which the complex hybrids are heterozygous increase in size, from three chromosomes in the Pigeon Rock $\odot 6$, through to seven in the $\odot 14$ s. The changes, from outbreeding to inbreeding through to the adoption of complex hybridity and increasing ring size, are mirrored by corresponding changes in heterozygosity, genetic debilitation and competitive ability (Table 3).

Table 3

Summary of *Isotoma petraea* breeding system and morphological adaptive responses to changes in genetic system.

	Primitive Forms		Pigeon Rock		Complex Hybrids
Cytology	7II	7II	7II	⊙6	⊙10-⊙14
Stigma Protrusion	High	Low	Very Low	Very Low	Variable
Observed Heterozygosity	Low	Low	Low	Medium	High
Competitive Ability	High	Low	Low	Medium	High
Debilitation	Low	High	High	Low?	None Expected
Interpopulational Heterosis	Low	High	n/a	n/a	Negative
Hybrid Instability	Yes	Yes	?	?	Yes
Flower Size	Large	Large	Large	Medium	Small
Ovule Number	Low	Low	Low	Low	High
Seed Aborting Lethals	Low	Low	Low-Medium	Medium-High	High, Early

Second, complex hybrid plants are characterised by a smaller flower size than 7IIs (James 1982a), a trend evidenced even within the Pigeon Rock population where there is a distinct floral dimorphism dependent on the genetic system (Table 3). A reduction in flower size is commonly associated with autogamic pollination (Jarne & Charlesworth 1993) and presumably represents the loss of a function (attraction of pollinating vectors) where such a function is irrelevant.

Third, the accumulation of chromosomes into interchange rings in complex hybrids results in meiotic irregularities and reduced gametic fertility (Darlington 1958; James 1970; Cleland 1972). Gamete fertility, 100% in 7II forms, is reduced to about 70% in ⊙6s and about 20% in ⊙14s. Fully half of the selfed progeny from the remaining gametes would be homozygous for the complexes and therefore not viable, so the potential fecundity of the ⊙14s is about 10% that of the 7IIs. Despite this loss of fecundity, the proportion of fully heterozygous progeny in complex heterozygotes is still higher for all ring sizes than for 7IIs (James 1970). The loss of fecundity is compensated for, in complex heterozygotes, by a substantial increase in ovule numbers (Table 3). A study of seven 7II and sixteen complex hybrid populations (Kiew 1969) showed that the 7II plants had an average of 1130 ovules per flower, while the complex hybrids averaged 1545. The Pigeon Rock ⊙6 had an average ovule number of 1090, a figure close to the average for the 7II populations, and to that for alethal Pigeon Rock 7IIs (JD Bussell unpublished data).

Fourth, the complex homozygote elimination system shows significant evolutionary development amongst *I. petraea* complex hybrids (Lavery & James 1987). The recessive seed aborting lethals which removed the SS complex homozygotes in the Pigeon Rock ⊙6s were relatively late acting so that the aborted seed exhibited a well developed but collapsed testa. As rings become larger, and as distance from Pigeon Rock increases, the time of seed abortion becomes earlier and earlier, so that in some large ringed forms, the aborted seeds are barely distinguishable from unfertilised ovules (Table 3). Earlier seed abortion allows fewer resources to be invested into incompetent seed. In some populations, homozygote elimination is based on complementary gametic lethality so that no resources are invested into incompetent complex homozygotes.

Distribution and Generation of Variation

The profound genetic system change, from relatively open sexuality to essentially invariant complex hybridity, might well be expected to be associated with a redistribution of variation within the population system (e.g. Darlington 1958; Jarne & Charlesworth 1993). This has been studied by examining the distribution of phenotypic variation within and between populations of *I. petraea* (Kiew 1969; SH James unpublished data). Patterns of variation were found to be dependent on the genetic system and on the selective importance of the character under examination, as detailed below.

The distribution of variance for ovule number, a character directly linked to the reproductive capability and fitness of plants, is strikingly different in the 7IIs and complex hybrids (Fig 1). In the 7IIs, most variance for ovule number occurs between populations, there is little between plants and very little between flowers within plants. Amongst the complex hybrids, on the other hand, most variance for ovule number occurs between plants within populations – the level at which selection occurs. Complex hybrids also have a significant amount of variation within plants. The complex hybrids' uniformly higher ovule number suggests that directional selection for ovule number is very strong in complex hybrid populations and less so among the 7IIs. Presumably this elevated ovule number is a response to the considerably reduced probability of an ovule becoming a seed, as described earlier.

In contrast, for metric characters (including leaf shape and the length of the peduncle) which have no obvious bearing on reproductive capability, the variance within the primitive 7IIs is distributed almost equally between populations, between plants within populations, and within plants (Fig 1). Amongst the derived complex hybrids, however, the variance between populations is relatively larger, and the variance between plants within populations, and within plants, is reduced.

The expression of phenotypic attributes is a complex process determined by the interaction of many genes. Characters which show constant expression, and therefore low levels of within plant variation, are said to exhibit a high degree of canalization, or homeostasis. Characters exhibiting higher levels of within plant variation are determined by less well canalized gene systems. Evolutionary change of a homeostatic character

can only be achieved when the canalizing gene systems are destabilised so that selectable variation becomes exposed in the population.

In general, heterozygous genotypes tend to exhibit more homeostatic control than homozygous genotypes (e.g. Mitton & Grant 1984; Palmer & Strobeck 1986; Jarne & Charlesworth 1993). However, wide crosses, as well as inbreeding, may lead to the destabilisation of developmental processes (Clarke 1994; Freeman *et al.* 1994). These observations may explain how the complex hybrids, with generally optimum levels of enforced heterozygosity, have a relatively lower within plant variance for metric characters than the inbreeding 71ls (which are more homozygous for a range of deleterious mutations), and yet have a higher proportion of within plant variance for ovule number than the 71ls (Figure 1).

In any population there is a fine balance between rigid control of developmental processes and maintenance of adaptive capacity. *I. petraea* offers a superb resource for studies into the effect of varying degrees of inbreeding and homozygosity on developmental processes and phenotypic variability in plants. Despite abandonment of recombination often being described as an evolutionary dead end (Darlington 1958; Carson 1967; Wagner & Gabriel 1990), important selectable diversity may still be generated in *I. petraea*, even in complex hybrids. Perhaps, along with hybridisation and the vestiges of sexual recombination and segregation, other more primitive mechanisms are utilised for genetic diversification and genome reorganisation. In particular, mobile genetic element activity destabilises the genome, it may affect particular parts of the genome more than others, and it may be promoted by "genomic shock", where mutually uncoadapted genomes are combined in wide crosses.

Conclusions

The network of granite rocks characterising large areas of the Australian continent are of particular importance as museums for relict flora, fauna, and of evolutionary processes. They provide a living collection of discrete yet integrated natural evolutionary experiments which generally so far have been sampled in only the most cursory fashion. Resolution of the evolutionary pathway leading to complex hybridity in *I. petraea* has provided a unique perspective on the consequences of inbreeding. Competition experiments reported herein, and previous work (Beltran & James 1974), have demonstrated distinct competitive advantages at critical stages in the proposed evolutionary pathway. At a more fundamental level, the *I. petraea* story supports the theory that biparental sexual reproduction and meiotic recombination are primarily concerned with genetic repair. Impediments to these processes result in the accumulation of deleterious mutations, genetic load, inbreeding depression and debilitation of whole populations. Importantly, and contrary to classical expectations, inbreeding, and especially intense inbreeding, does not purge the genetic load. Load in *I. petraea* may be managed either by outbreeding or, in inbreeding populations, by the early elimination of incompetent homozygotes and strict control of recombination via complex hybridity.

Interpopulational hybrids and the naturally occurring complex hybrids demonstrate considerable variation (decanalization) for morphological and reproductive characteristics and for competitive ability. These hybrids are comparable in many ways to the mutator genotypes generated by interracial hybrids of *Drosophila* (Thompson & Woodruff 1978), some of which induce mobile genetic element activity (Fontdevila 1988). It seems likely that mutator genotypes, generated by interfacing separately co-adapted gene pools, release an innovative capability which is more primitive than the genetic innovation associated with diploid sexuality, and which has been, and still is, of profound importance in organic evolution. This harks back to Darlington (1956) who, in discussing the nature of variation in natural systems, concluded that the genome's ability to generate biological capability and variability must be more important in enabling biological evolution than the environmental factors promoting it. The possible role of mobile genetic elements in mutator genotype activity in *I. petraea* remains to be investigated.

It is hoped that this paper has presented a picture of the granite rocks scattered throughout arid Australia, not so much as self-contained inselbergs to be managed and conserved as isolated units, but as networking subdivisions of species' metapopulations and as places of active, documentable evolutionary change. They are ideally suited, as museums of evolutionary processes, for the study of genetic behaviour, variation and evolutionary responses. *I. petraea* has proved to be most illuminating in the study of these phenomena, and will no doubt continue to be so.

I. petraea has been instrumental in the development of an understanding of the presence and action of seed aborting lethal genes in many of Western Australia's signature floral genera, including *Stylidium*, *Anigozanthos*, *Drosera*, *Laxmannia* and *Eucalyptus* (reviewed by James 1982a,b, 1992, 1996; Burbidge & James 1991). Recently, Kennington & James (1997) have outlined a mechanism whereby recessive lethal and mildly deleterious genes may interact to prevent purging of load in eucalypt species. Study of *I. petraea* has also helped elucidate notions of genomic coalescence as a potent evolutionary force (reviewed by James 1992). Pigeon Rock, set in the midst of superb, relatively undisturbed country, is of considerable importance as the putative origin of complex hybridity in *I. petraea*. This inselberg warrants special conservation status, including removal of the present stockyards, exclusion from the surrounding pastoral lease and preclusion of vermin. In fact, we feel that Pigeon Rock warrants World Heritage listing.

Acknowledgments: We thank N Cohen, J Playford, L P Kiew and R Tinetti for data currently residing in unpublished honours dissertations at the Department of Botany, University of Western Australia. Thanks are due also to M Waycott, J Kennington, and H Stace for discussions and comments on the manuscript.

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The ant communities of Sanford Rock Nature Reserve, Westonia, Western Australia

A I Doronila & J E D Fox

School of Environmental Biology, Curtin University of Technology,
GPO Box U1987, Perth WA 6845;
email: idoronil@info.curtin.edu.au

Abstract

This study investigated the ant communities present in the Sanford Rock Nature Reserve (325 mm mean annual rainfall, 300 km East of Perth), an 800 ha Reserve comprising a complex mosaic of granite outcrop and tumbled boulders with surrounding flat areas carrying woodlands or shrublands. Nine locations in the reserve and two others in a eucalypt woodland 9 km away were sampled with pitfall traps and hand collection during March of 1994–1996. A total of 87 ant species from 22 genera was recorded. Three genera, *Iridomyrmex* (22 species), *Camponotus* (12 species) and *Melophorus* (11 species) represented 51.7% of the total species composition, which is typical of ant communities in arid and semi-arid Australia. Ant species richness (>30) was greatest in *Eucalyptus* woodlands with mixed shrub understorey species. The *Callitris* and *Acacia* low shrub thicket were represented by 18 and 21 species respectively. Thickets with *Allocasuarina* or *Eucalyptus crucis* had the lowest species richness (< 15). These thickets were in deep soil pockets which were moist and contained large amounts of litter. Hot climate specialist ants were poorly represented in the species poor areas.

Introduction

Westonia is a small agricultural and gold mining district 285 km east-north-east of Perth, Western Australia (31° 40' S, 118° 35' E). The district has been extensively cleared for wheat growing and sheep grazing and the nearest piece of remnant vegetation is 9 km north-east of the town at the Sanford Rocks Nature Reserve (800 ha). The reserve is in very good condition as it has been fenced off from cattle and sheep grazing and there have been no fires in nearly all of the reserve since at least 1927 (Muir 1979). This area experiences a Mediterranean climate typical of the wheatbelt regions. Summer thunderstorms occur occasionally but most of the rainfall occurs during winter. The average annual rainfall is 325 mm.

The role of fauna within mature and developing ecosystems situated on previously disturbed land is often neglected. There is a paucity of long-term studies on fauna recolonization (Majer 1989). Ants are one of the most important invertebrate groups in Australia especially in seasonally arid regions (e.g. Westonia). They are useful as bio-indicators of change in the environment (Andersen 1990; Majer 1983). Ant community structure is influenced by interaction with their habitat, mainly with the vegetation complex (Andersen 1986).

The aim of this study is to assess the ant communities present on several of the vegetation communities and to determine the factors influencing the patterns of their community organisation.

Methods

Site selection

Ants were sampled annually from 1994–1996 on eleven transects. Nine sites were sampled in the reserve. These were; (Eg) grass-eucalypt woodland boundary *Eucalyptus capillosa* woodland with sparse herb understorey of *Amphiphlogon strictus*; (Sg) salmon gum woodland with *E. salmonophloia*, *E. sheathiana* and *E. myriadena* with an *Acacia* and chenopod understorey; (Th) *Acacia* scrub thicket on rock edge; (Gw) *E. salubris* and salmon gum, *E. salmonophloia* woodland with a sparse chenopod understorey; (Al) *Allocasuarina luegeliana* thicket; (Yg) *E. loxophleba*, *E. myriadena* and *E. salmonophloia* woodland with a sparse understorey of *Acacia*, *Melaleuca*, *Borya* sp; (Cx) *E. crucis* thicket with dense understorey of *Kunzea* and *Calothamnus*; (Ov) overhang with mixed *Acacia* and Myrtaceae shrubs; and (Ct) *Callitris columellaris* thicket.

Two other locations were sampled 9 km away from the reserve. The disturbed site (Ewd) is situated at the eastern end of the Westonia town-site where the hospital was situated 70 years ago. It is a *Eucalyptus* woodland of 15–20 m in height. The upper canopy is dominated by *E. longicornis* and *E. salubris* with a sparse understorey of *Acacia hemiteles* and chenopod shrubs. The undisturbed woodland (Ewu) is situated at the town commons. The vegetation is a *Eucalyptus* woodland dominated by *E. salubris* and the understorey is a dense association of *Acacia* and *Melaleuca* species.

Sampling methods

Ants were sampled using pitfall traps (1.8 cm diameter Pyrex®) which were partly filled with a 30:70 glycerol : alcohol mixture). Each location was sampled with a transect of ten traps with 10 m spacing and operated for a 1 week period during mid-March. Hand collections

Table 1
The number of ant species collected in the study at Sanford Rock Nature Reserve.

Area ¹	Sanford Rock Nature Reserve								Non reserve		
	Thickets					Eucalypt woodland				Ewu	Ewd
	Cx	Ov	Al	Th	Ct	Eg	Gw	Yg	Sg		
Myrmeciinae											
<i>Myrmecia</i>									1	1	1
Ponerinae											
<i>Bothroponera</i>						1	1		1		
<i>Rhytidoponera</i>	2		1	1	3	3	3	2	3	3	4
<i>Odontomachus</i>					1		1		1	1	
Myrmicinae											
<i>Crematogaster</i>							1		1		
<i>Aphaenogaster</i>					1				1		1
<i>Cardiocondyla</i>										1	
<i>Monomorium</i>	1	2	5	4	2	6	1	7	6	4	6
<i>Meranoplus</i>					1			1	2	2	1
<i>Pheidole</i>		2	1	2						1	2
<i>Tetramorium</i>			3	1			1	2		1	3
<i>Podomyrma</i>				1				1			
Pseudomyrmecinae											
<i>Tetraponera</i>						1			1		1
Dolichoderinae											
<i>Iridomyrmex</i>	4	5	1	2	5	6	10	6	9	12	8
<i>Papyrius</i>									1	1	
Formicinae											
<i>Calomyrmex</i>					1	1	1		1	1	1
<i>Camponotus</i>	2	1		2	4	5	5	7	8	6	7
<i>Melophorus</i>		1	2	5	3	7	7	5	8	3	7
<i>Notoncus</i>											1
<i>Ophiotopsis</i>								1			
<i>Polyrachis</i>						1	1	1	1	1	
<i>Stigmatoceros</i>										1	
TOTAL SPECIES	9	11	13	18	21	31	32	33	45	39	43

¹ants listed by subfamily (bold) and genus (italic).

were also performed for uniform periods during the day. Ants were sorted to genera and a number or letter code was allocated to each specimen which applies only to this study. The vegetation composition, cover, density, percent leaf litter cover and percent bare ground were measured at equidistant intervals along each transect.

Results and Discussion

A total of 87 ant species from 22 genera was recorded (Table 1). Three genera, *Iridomyrmex* (22 species), *Camponotus* (12 species) and *Melophorus* (11 species) represented 51.7% of the total species composition which is typical of ant communities in arid and semi-arid Australia (Greenslade 1976; Andersen 1983). Classification of ants into functional groups (Andersen 1990; Greenslade 1979) shows that dominant ant species (*Iridomyrmex*) contributed 20–30% to the diversity of the communities with high species richness (Fig 1). Dominant species also contributed > 60% of the total catch where they were present in high frequencies.

Ant species richness (>30) was greatest in *Eucalyptus* woodlands with mixed shrub understorey species. The *Acacia* low shrub and *Callitris* thicket were represented by 18 and 21 species respectively. Thickets with *Allocasuarina* or *Eucalyptus crucis* had the lowest species

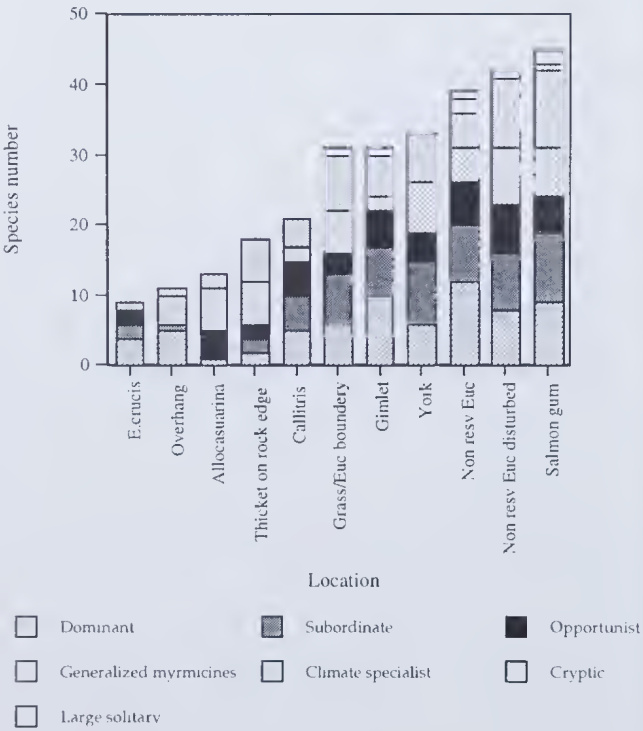


Figure 1. Classification of ant communities present in the 11 sites by functional groups.

richness (< 15). These thickets were in deep soil pockets which were moist and contained large amounts of litter. Hot climate specialist ants *e.g.* *Melophorus* and *Meranoplus* species were poorly represented in the species-poor areas.

Ordination of the presence and absence data of ants in each transect was performed, and axes 1, 2 and 3 represented 24.6, 14.8 and 13.1% of the total variance, respectively.

Three main groupings could be identified from the ant assemblages;

- sites with eucalypt woodlands but with two identifiable subgroups of the reserve and non-reserve areas; *Callitris* thicket appeared to be similar to these sites;
- the *Acacia* scrub and *Allocasuarina* thickets were similar; and
- the *E. crucis* and overhang area were similar.

Factors which appeared to be important to ant species richness were tested. A negative correlation was observed between the number of ant species and percentage litter cover ($r = -0.559$) and vegetation cover ($r = -0.542$). Many factors such as soil moisture, depth of litter, density of ground vegetation and soil type determine the availability and suitability of nest sites and foraging behavior. These factors consequently affect the diversity of ants in an area (Greenslade 1979).

Acknowledgments: We thank the students involved in the Terrestrial Ecology 301 field trips who participated in various aspects of the study.

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Acacia williamsiana (Fabaceae: Juliflorae): A new granitic outcrop species from northern New South Wales

J T Hunter

Department of Botany, University of New England, Armidale NSW 2351
email: jhunter@northnet.com.au

Abstract

Acacia williamsiana J.T. Hunter a new rare species (2RCa) restricted to granitic outcrops within the New England Batholith is described. This species is known from four disjunct localities within the North Western Slopes botanical division in New South Wales.

Introduction

During the compilation of a preliminary checklist of the flora of Kings Plains National Park on the north western slopes of New South Wales by John Williams, an unidentifiable specimen of *Acacia* was collected. This taxon was collected again from Kings Plains National Park by the author during an extensive survey of the granitic outcrop flora of the New England Batholith. Further collections of material that match this taxon were made during this survey on granitic outcrops within Severn River Nature Reserve and the proposed Kwiambal National Park. Subsequently a population was also discovered on a granite outcrop by the author, during an inspection of a new fire trail within the Torrington State Recreation Reserve.

Acacia williamsiana at all localities was restricted to granitic outcrops or around the base of outcrops. This taxon often dominated habitats where it was found, sometimes forming monospecific stands.

Materials and Methods

This study is based on examination of materials collected by the author and others at all known localities of this taxon. All measurements were made from dried specimens.

Taxonomy

Acacia williamsiana J.T. Hunter, sp. nov.

Acacia williamsiana, species nova similis *A. bulgaensis* Tind. & Stuart J. Davies a qua ovarium glabris, pedunculus brevissimus, et juvenis phyllodium glabris.

Typus: New South Wales: North Western Slopes: on the banks of Kings Plains Ck, in Kings Plains National Park, north-west of Glen Innes, J.T. Hunter 4112 & P.J. Clarke, 1 November 1996 (holo: NSW; iso: AD, BRI, HO, MEL, NE, PERTH).

Tall shrub to small tree 2–8 m tall, often spreading

widely when young then becoming fruticose and eventually erect; *Bark* fissured and flaky, grey to dark grey-brown; *branchlets* angular, flattened to ellipsoid in section, glabrous, ± glaucescent, yellow-orange to red-brown. *Phyllodes* borne singly, diphyllous; phyllodes on young plants broad elliptic to obovate, sometimes slightly falcate, often held horizontally, 1.3–7.5 cm long, 1.3–2.5 cm wide, pale green almost glaucous in appearance, glabrous; longitudinal nerves 60–100 per phyllode, with 3–5 more prominent; apex obtuse with a broad ± oblique callous mucro; mature phyllodes oblanceolate, linear, elliptic to narrow elliptic, rarely slightly falcate, held erect, 4.5–12 cm long, 0.4–1.1 cm wide, pale green to subglaucous, glabrous or rarely pilose and glabrescent; longitudinal nerves 20–60 per phyllode, with 3–5 more prominent; apex acute with a distinct ± oblique callous mucro, 0.5–3.5 mm long; *gland* 0 or 1, obscure ± hairy, 0–0.5 mm from pulvinus, orifice elliptical; *pulvinus* 0.5–3 mm long, wrinkles transverse, pale; *stipules* 2, 0.3–1 mm long, triangular, often caducous, ± pilose. *Inflorescences* spicate, borne in pairs one on either side of the phyllodes, sessile, initially curved, 1.5–4 cm long in fruit, glabrous or rarely hairy basally, > 150 flowers per spike, pale yellow; *bracts* 2, glabrous, pilose or pubescent, 1.2–2.5 mm long, 1–1.7 mm wide, ± caducous; *pedicels* lacking; *buds* broad ovate; *stipe* 0.5–1.5 mm long in fruit; *bracteole* 0.7–0.9 mm long, pale brown, distinctly clawed, the lamina perpendicular to the claw, tomentose apically and abaxially. *Flowers* 5-merous; *calyx* fused, tube 0.7–1.2 mm long, lobes minute ca. 0.1 mm long, silver woolly to tomentose, more so basally; *corolla* valvate, fused about half way or more, tube 1–1.5 mm long, lobes 0.8–1.2 mm long, glabrous, minutely clawed; *stamens* with filaments 1.7–2.5 mm long; *anthers* versatile, 0.1–0.15 mm long; *ovary* ellipsoid, 0.2–0.5 mm long, 0.2–0.4 mm wide, green, hairy, viscid; *style* 1–2.5 mm long, stigma minutely lobed. *Legumes* linear, falcoid but not curled, ± constricted between seeds, 3.5–9 cm long, 2–4 mm wide, brown, ± glaucescent, wrinkled, margins thickened, turgid when young and fresh becoming flat. *Seeds* 6–12 arranged longitudinally in legume, ellipsoid, 0.6–1 mm long, 0.3–0.6 mm wide, dark brown to black; *funicle* filiform, folded 2–3 times. Fig. 1.

Specimens examined. New South Wales: North Western Slopes: Kings Plains Ck, Kings Plains National Park, J. T. Hunter 1866 & V.H. Hunter, 27 April 1994 (NE);



Figure 1. A—H, *Acacia williamsiana*. A, adult branch with flower buds. B, young branch. C, adult branch with flower buds. D, venation pattern of phyllode. E, pulvinus and gland. F, adult branch with pods. G, flower. H, inflorescence. Scale bars; A, B, C, F = 4 cm; D = 7 mm; E = 4 mm; G = 2 mm; H = 13 mm. Drawn from J.T. Hunter 3933 (A); J.T. Hunter 2888 (B); J.T. Hunter 2934 (C, D, E); J.T. Hunter 4113 (F); J.T. Hunter 4114 (G, H). Drawn by D Mackay.

Kings Plains, 1 km N of Falls, 50 km NW of Glen Innes, *J.T. Hunter* 2888, 9 March 1995 (NE); 10 km W of Torrington on the Buther Rd, *J.T. Hunter* 3931–3935, 4 May 1996 (NE JTH 3931; BRI JTH 2932; NSW JTH 3933; MEL JTH 3935); 29.3 km from Emmaville on the Gulf Rd, *C. Nano & J.B. Williams s.n.*, 13 December 1996 (NE); Severn River Nature Reserve, NE of Glen Innes, near Pindari Dam, *J.T. Hunter* 3112, 13 June 1995 (NE); Severn River Nature Reserve, NE of Glen Innes, near Pindari Dam, *J.T. Hunter* 3142, 14 June 1995 (NE); McIntyre Falls, Kwiambal National Park, W of Ashford, *J.T. Hunter* 4114 & *P.J. Clarke*, 1 November 1996 (BRI, MEL, NE, NSW, PERTH); McIntyre Falls, Kwiambal National Park, W of Ashford, *J.T. Hunter* 4113 & *P.J. Clarke*, 1 November 1996 (NSW).

Distribution. This species has been found in four disjunct localities on the north western slopes of New South Wales; Kings Plains National Park 40 km north-west of Glen Innes, Severn River Nature Reserve 50 km north-west of Glen Innes, Torrington State Recreation Reserve 60 km north-north-west of Glen Innes and the proposed Kwiambal National Park and adjacent Severn State Forest 30 km west of Ashford.

Habitat. Found in open and exposed situations in shrubland and low woodland on and around the base of granite and porphyry outcrops between 280–1100 m altitude. The mean annual rainfall in these areas is between 640–800 mm. This taxon is found within crevices of bare rocky slopes and shallow soil surrounding the bare slopes. This species often forms thick stands when mature, and can dominate or co-dominate communities in which it is found. Associated species include *Callitris endlicheri* (Parl.) F.M. Bailey, *Eucalyptus prava* L. Johnson & K. Hill, *E. caleyi* Maiden, *E. dealbata* A. Cunn. Ex Schauer, *Allocasuarina inophloa* (F. Muell. & Bailey) L.A.S. Johnson, *A. brachystachya* L.A.S. Johnson, *Micromyrtus grandis* J.T. Hunter, and *Astrotricha roddii* Makinson.

Flowering and fruiting. September to December

Conservation status. A ROTAP code of 2RCa (Briggs & Leigh 1988) is suggested. This species has a disjunct distribution and is known only from four localities and from a restricted habitat, on and around the base of granitic outcrops. Therefore this species is considered to be rare. All known populations are within some form of reservation under the control of the New South Wales National Parks and Wildlife Service.

Etymology. The specific epithet is in honor of Mr

John B. Williams former lecturer and now honorary fellow at the University of New England, Armidale, NSW. Mr Williams has worked extensively in the north-east of New South Wales, particularly on granite flora and was the first to find and note this species as a potential new taxon.

Notes. This taxon has a diverse appearance both in terms of habit and phyllode form. Comparatively young plants have a divaricate habit with phyllodes that are short and broad (Fig 1). Adult plants have a tall and straight habit with long thin phyllodes that are held erect. Forms at intermediate stages are often present. This species is killed by fire and seedlings appear readily afterwards. Seedlings, however, do not seem to be present unless a disturbance such as fire has occurred. Consequently individual populations are usually the same cohort grown after single wildfire events. Only where fire has passed differentially over outcrops are mixed aged populations found. The affinities of this species are unclear at this stage. However, it is possible that they are near *A. bulgaensis* Tind. & Stuart J. Davies and *A. diphylla* Tind.

Conclusion

Acacia williamsiana is a distinct species endemic to granitic outcrops of the New England Batholith. Other members of the Juliflorae growing on the New England Batholith are granitic outcrop endemics, such as *A. pycnostachya* F. Muell. and *A. pubiflora* Pedley. Others of the Juliflorae while not restricted to outcrops, are commonly found on them. Further work on the phylogenetic and biogeographical relationships of this species and its relatives is warranted.

Acknowledgments: The author wishes to thank the director of the NSW National Parks and Wildlife Service for allowing collection of materials within service areas. B Briggs is thanked for allowing access to specimens at NSW. Thanks also to J B Williams for discussions, the staff of the Glen Innes office of the NSW National Parks and Wildlife Service for their assistance, D Mackay for illustrations, and J J Bruhl and P J Clarke for supervision. The author acknowledges the receipt of an Australian Postgraduate Award scholarship.

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History and management of Culham Inlet, a coastal salt lake in south-western Australia

E P Hodgkin

86 Adelma Road, Dalkeith, WA 6009

email: ehodgkin@cygnus.uwa.edu.au

Manuscript received August 1996; accepted May 1997.

Abstract

When Culham Inlet was first flooded by the Holocene rise in sea level it was an estuary, but in historic times it has been a salt lake closed by a high sea bar. It is in an area of low rainfall and episodic river flow and sometimes all water is lost by evaporation to below sea level. With above average rainfall in 1989 and 1992, high water levels in the Inlet flooded farm paddocks and threatened to break the bar and a road along it from Hopetoun to the Fitzgerald River National Park. In 1993 the bar was breached to release flood water, and the Inlet was briefly an estuary. Engineering measures designed to restore road access and prevent flooding are examined for their potential to restore the Inlet to its pre-1993 condition of a productive ecosystem. Recent clearing in the catchments of Culham Inlet and nearby estuaries in the south coast low rainfall area has increased river flow to them and appears to have caused their bars to break more frequently.

Introduction

In historic times Culham Inlet has been a coastal lagoon on a semi-arid part of the south coast of Western Australia (Fig 1), separated from the sea by a high bar

(Fig 2) that is only known to have broken naturally once, in 1849. The bar was broken artificially in 1920, but for over 70 years since then the Inlet has absorbed river flow without the bar breaking, until 1993. Culham Inlet was a

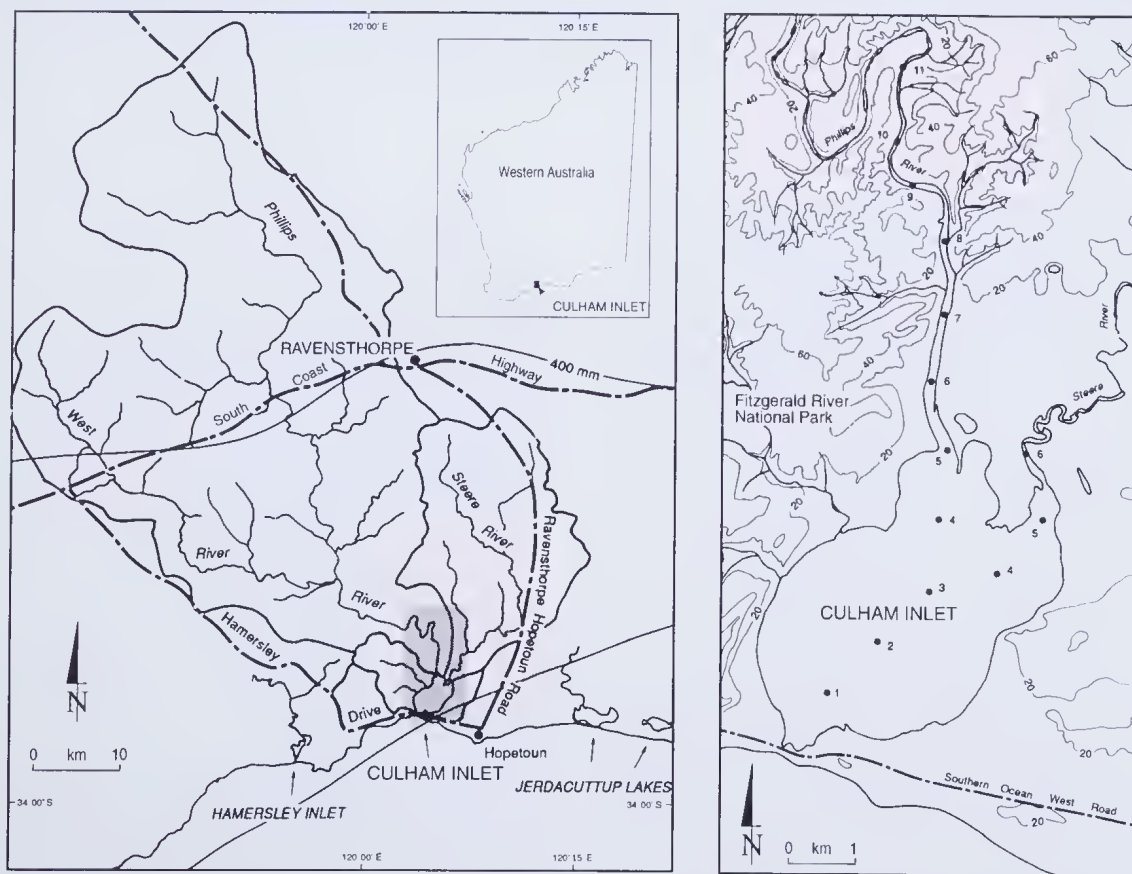


Figure 1. Culham Inlet; the catchment with 400 mm isohyet (left) and plan of the Inlet (right).

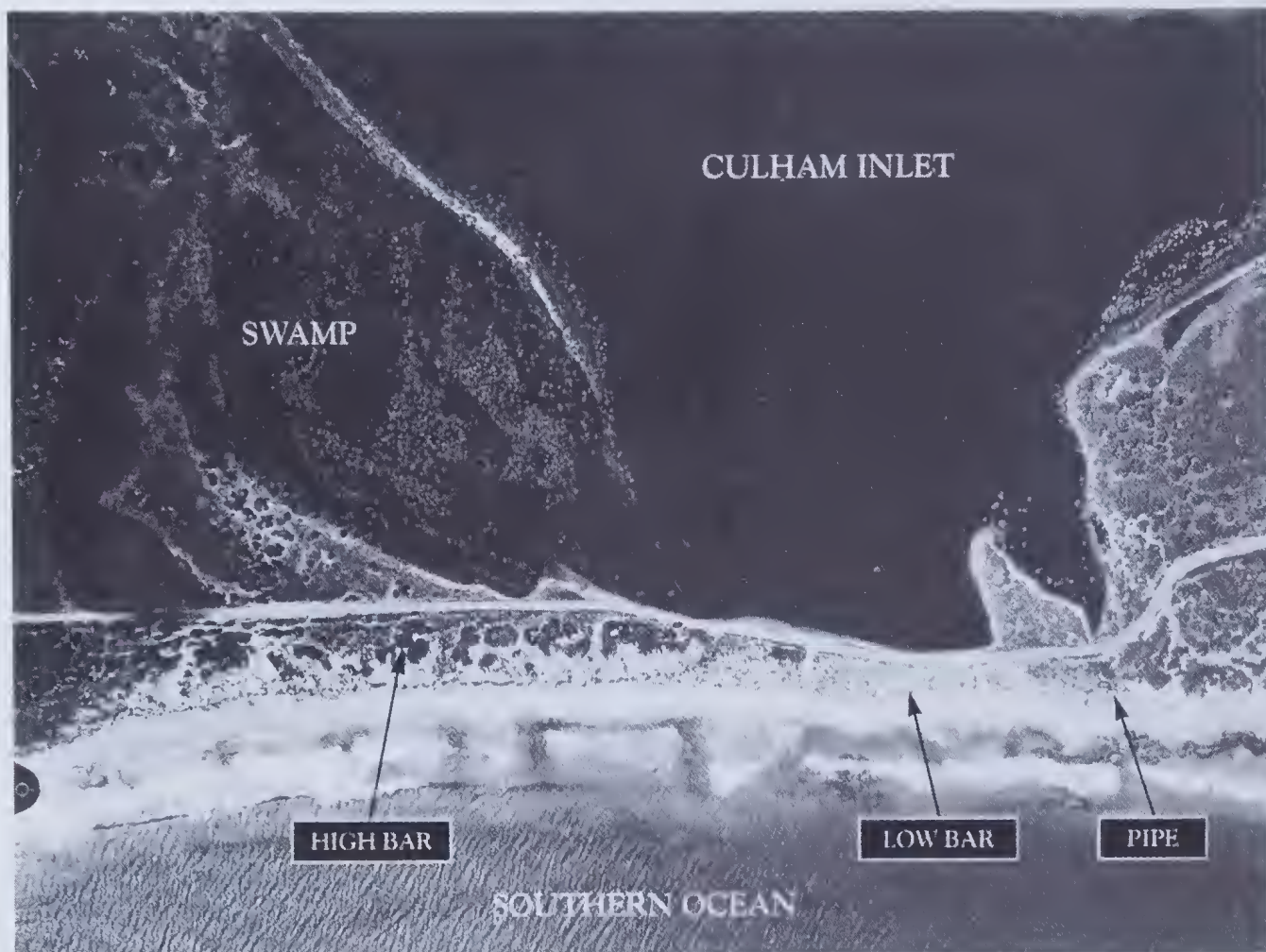


Figure 2. Culham Inlet bar/dune area, January 1990; water level at 2.5 m AHD. Scale 1:8000 Photograph from the Department of Land Administration, Perth; Copy Licence 509/96.

salt lake where water depth varied from 5 m to none, depending on episodic flow from two saline rivers and evaporation. Ecologically, it supported a restricted range of 'estuarine' fauna, sometimes with an abundance of a few species of fish and large numbers of waterbirds (Hodgkin & Clark 1990).

A road along the bar gave access from Hopetoun (population 206, 1991 Census) on the east to the Fitzgerald River National Park to the west, but in 1989 and 1992 floods closed the road and inundated nearby low-lying paddocks. The town's growing tourist industry suffered and there was social and economic pressure to ensure reliable road access and prevent flooding. In May 1993 the high water level in the Inlet again caused flooding and threatened to breach the bar. An attempt to release flood water without the bar breaking failed; it broke and the Inlet was effectively an estuary for a few weeks until the breach closed. Several engineering measures to rebuild the road and prevent flooding were proposed, and one was implemented in 1996-97. The unpredictability of rainfall, the limited data on river flow, and the probability that recent clearing in the catchment has considerably increased river flow to the Inlet all make it difficult to assess the environmental consequences of the various proposals to rebuild the road and the extent to which the Inlet can now revert to being a productive coastal lagoon.

The Environment

Culham Inlet is an 11 km² lagoon about 1 m deep below mean sea level (Fig 1B). Seven km of the Phillips River are scoured in places to 4 m below sea level, and there is a river delta at about sea level. All levels quoted here are relative to Australian Height Datum (AHD) which is 0.089 m above MSL (an accurate tidal datum was established in January 1990). The mean daily tide range is 0.67 m (MHHW to MLLW) at Hopetoun. Inlet water level varies greatly with river flow and evaporation, from +4 m to -1 m (no water). The salinity of lagoon water varies from 10 to >70 ppt. Tributary river water is seldom <5 ppt, and stagnant river pools can be hypersaline to sea water (Hodgkin & Clark 1990).

The barrier between the lagoon and the sea is a 1 km long bar, now with a dune built on it (Fig 2). The western part is a 10-15 m high dune, 100 m wide, with trees and shrubs. The eastern 400 m is 4 to 5 m high, 40-60 m wide, and sparsely vegetated.

Catchment rainfall ranges from 500 mm at the coast to 350 mm inland (Fig 1A). The only long-term (100 years) rainfall data are for Ravensthorpe and Hopetoun, both just outside the catchment. Winter rainfall is relatively reliable with 60-70% falling in the 6 months May to October (Fig 3), but the summer rainfall means are boosted by infrequent heavy falls (>100 mm). There can

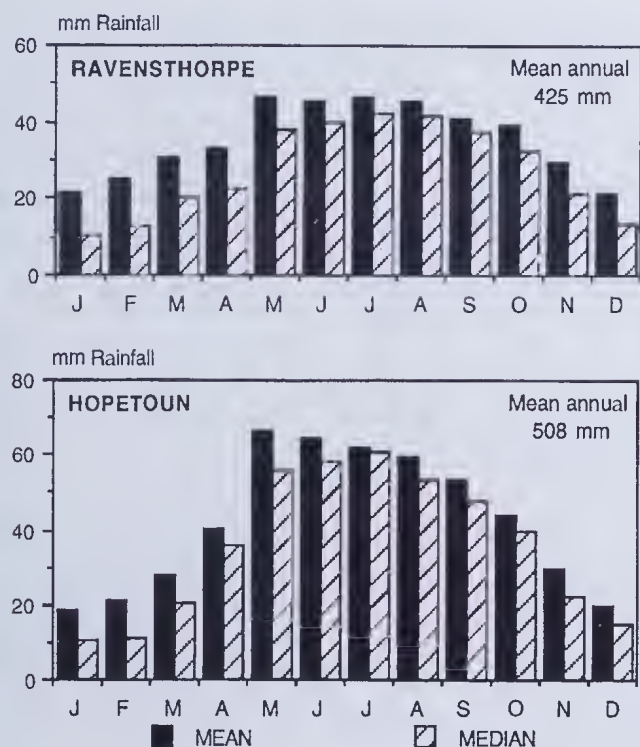


Figure 3. Mean and median monthly rainfall at Ravensthorpe and Hopetoun (1901-1993). Data from the Bureau of Meteorology, Perth.

be episodic 2-3 day falls of 50 to 100 mm in most months. A 50 mm fall, such as that of 6-8 October 1992, was estimated to recur every 7 years on average and that of 28-29 May 1993 every 2.5 years (Anon 1993a).

Mean annual pan evaporation is 1754 mm (at Esperance), but surface evaporation from the Inlet is probably only 85% of pan evaporation, as found in Peel Inlet by Black & Rosher (1980) and in reservoirs by Hoy & Stephens (1979). An estimate based on water level data in Culham Inlet and rainfall at Hopetoun (1990-1994) indicates that evaporation from the Inlet was about 1100 mm over the six summer months from November to April.

Two rivers flow to the Inlet (Fig 1), Phillips River with a catchment of 2100 km² and Steere River with 485 km². The Phillips catchment rises from sea level to about 300 m with extensive areas of sandplain and Precambrian rocks and a narrow belt of Quaternary coastal deposits (Thom *et al.* 1977; Thom & Chin 1984). Vegetation is predominantly mallee in inland areas and mallee-heath towards the coast (Beard 1972, 1973).

The rivers are not gauged, but effective annual flow probably varies from zero to $>50 \times 10^6$ m³, most of it as episodic events over a few days following heavy rain, as shown by the record of water level in the Inlet kept by R Cooper (Figs 4 & 5). The flow pattern is similar to that in the Pallinup River (Fig 6), the nearest river with a long gauged record.

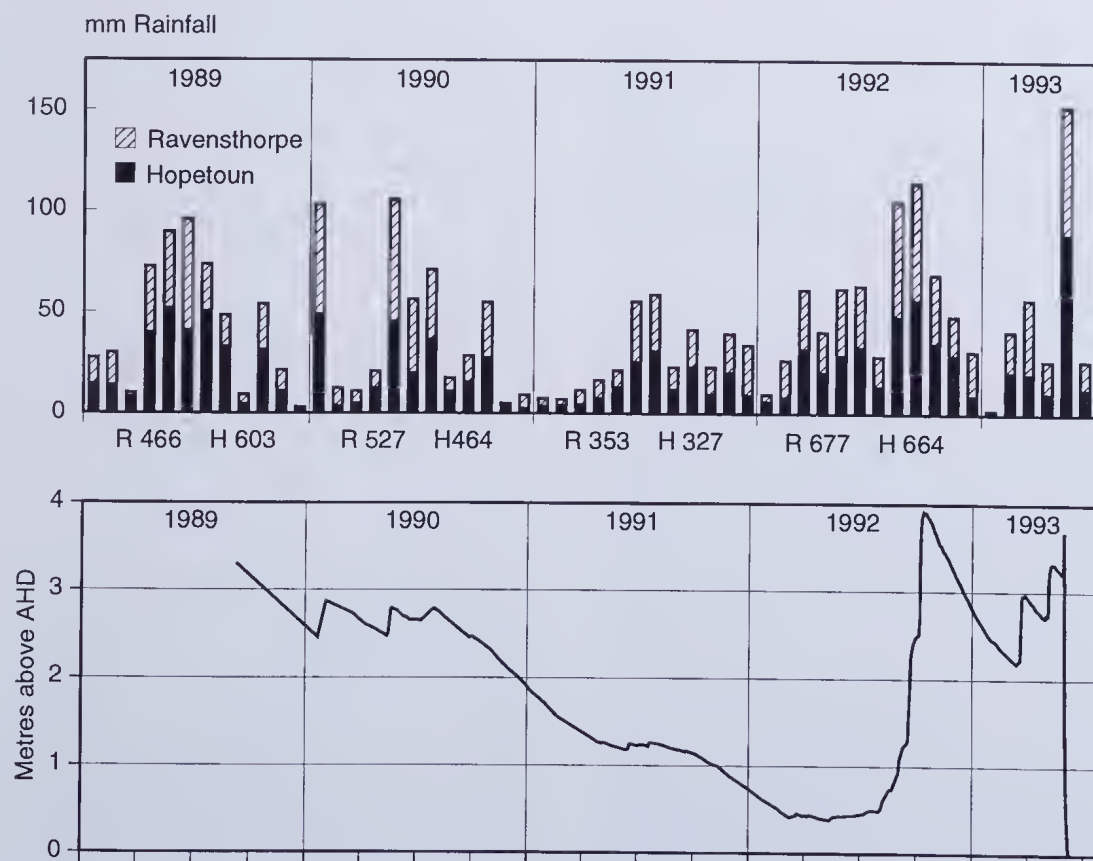


Figure 4. Top. Monthly and annual rainfall at Ravensthorpe and Hopetoun, 1989-1993 (mean annual rainfall: Ravensthorpe 424 mm, Hopetoun 506 mm). Data from the Bureau of Meteorology, Perth. Bottom. Water level in Culham Inlet 1989-1993. Data from R Cooper.

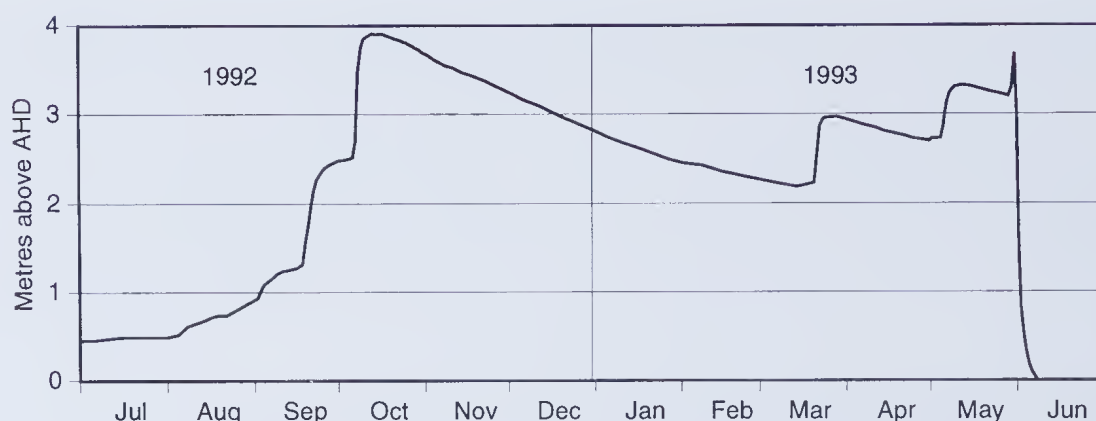


Figure 5. Water level in Culham Inlet from July 1992 to June 1993. Data from R Cooper.

The volume of river flow also varies greatly with soil moisture in the catchment. Nearly 300 mm of rain from February to July 1992 caused little flow from the dry catchment and no rise in Inlet water level (Fig 4). However that rain saturated the catchment, and in August to early October a further 300 mm of rain caused a rise in water level of 3.4 m. Only about 50 mm of rain on two days in October caused a rise of 1.5 m (about $15 \times 10^6 \text{ m}^3$ of river flow). The capacity of the Inlet to accept such flows without the bar breaking depends on the initial water level in the Inlet, which was only 0.5 m in July 1992 but was already 3.3 m in May 1993 (Fig 5).

The area of cleared catchment (estimated from aerial photographs) increased from about 10% in 1968 to 40% by 1988. There is no record of river flow to Culham, however mean annual flow is estimated to be $3.5 \times 10^6 \text{ m}^3$ and to have increased from $1.3 \times 10^6 \text{ m}^3$ before clearing (data from Surface Water Branch, Water and Rivers Commission, Perth), and it may continue to increase for some time. The loss of deep-rooted vegetation, reduced moisture percolation from soil compacted by stock, and rising groundwater levels all contribute to increased runoff from the semi-arid catchment.

The Biota

Before the bar broke in 1993, Culham Inlet was periodically a highly productive ecosystem. Commercial fishers took large catches of black bream (*Acanthopagrus butcheri*) in seasons when the water level remained relatively high and salinity was <45 ppt (32 tonnes in 1990-91; 61 t in 91-92; 77 t in 92-93; Fisheries Department, CAESS, Perth) and recreational fishers also took large numbers of bream. A goby (*Pseudogobius olorum*) and two hardyheads (*Atherinosoma clouga* and *Leptatherina wallacei*) were common. There were large waterbird populations with 25 recorded species. The few euryhaline estuarine species of macro-invertebrates were abundant: the encrusting tubeworm *Ficopomatus enigmaticus* and the false mussel *Fluviolanatus subtorata* (Trapeziidae), a few polychaete worms, two amphipods and midge larvae (Hodgkin & Clark 1990). After the brief period while the Inlet was tidal, additional estuarine-marine invertebrate species (*Ceratonereis* sp, *Spisula trigonella*) were found to be common and a few opportunistic species of fish were caught, notably sea mullet *Mugil cephalus* and herring *Arripis georgianus* (Bennett & George 1994).

The Inlet has a narrow fringe of salt-tolerant flora dominated by the paperbark *Melaleuca cuticularis* backed by coastal moort (*Eucalyptus platypus* var *heterophylla*), with yate (*E. occidentalis* var *occidentalis*), *Acacia cyclops*, and *Eucalyptus tetragona* on higher ground (Bennett & George 1994). The paperbarks and coastal moorts along the eastern shore of the Inlet died following the prolonged 1989-90 flooding with saline water (about 17 ppt). The previously limited areas of samphire (*Sarcocornia quinqueflora*) have expanded greatly while the water level has been low since 1993. The aquatic *Ruppia megacarpa* was present but seldom abundant.

History of Culham Inlet

Before the post-glacial rise in sea level, Culham Inlet would have been a valley with a river flowing through it; there is about 25 m depth of sand below present sea level at the bar (Anon 1993b). By 6500 years BP the rising sea level had flooded the Inlet, at least to its present level, and it remained an open estuary until about 3500 BP as evidenced by the abundant sub-fossil fauna of estuarine-marine molluscs dated $3660 \pm 185 \text{ BP}$ (Hodgkin & Clark 1990). With only episodic river flow from the semi arid catchment the bar built to a height at which it retained river flow, perhaps at first with periodic breaks as now at 'normally closed' estuaries such as Hamersley Inlet (Fig 1), before becoming a 'permanently closed' estuary (Lenanton 1974; Hodgkin & Lenanton 1981) i.e. a coastal salt lake. The western bar, now with a high dune, may have closed first and the eastern low bar later.

The bar is known to have opened naturally in 1849 (Gregory 1849) and is said to have broken in the 1870s. It was opened artificially in 1918 or 1920 when floods threatened to break it during eight years of above average rainfall (1913-20), and it is reported to have remained open for about three months. The break appears to have opened a 200 m wide gap through the eastern low bar where sea water is seen seeping into the almost dry Inlet in an aerial photograph of January 1981 (Fig 7). Above average rainfall in 1955 ($\approx 660 \text{ mm}$) again threatened the bar, and water is reported to have 'trickled out'.

By September 1988, runoff from above average winter rain had raised the Inlet water level to about 3 m, with 0.8 m of water over the road along the bar at its lowest point. Again in 1989 there was above average winter

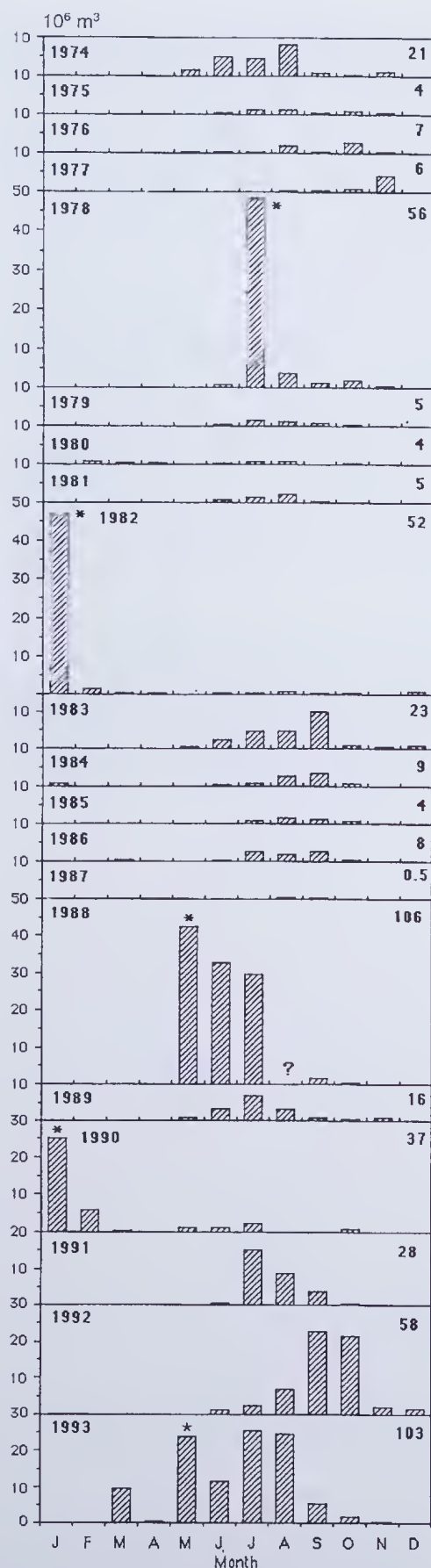


Figure 6. Monthly and annual flow (10^6 m^3) in the Pallinup River, from gauged catchment 602001 (3655 km^2). Data from the Water and Rivers Commission, Perth.

rain, the Inlet water level was about 3.3 m (Fig 4), roads and farmland were flooded, and paperbark trees and coastal moorts along the eastern shore of the Inlet died. In May 1990 a pipe of 900 mm internal diameter was installed in the eastern end of the bar, with an overflow level at 2.2 m (Anon 1993a). Rainfall was well below average in 1991, there was little river flow and Inlet water level continued to fall for the first seven months of 1992 to about 0.4 m. Early rain saturated the catchment soils and river flow from 300 mm of rain in August to October raised Inlet water level to 3.9 m (Fig 5). Water seeped through the bar/dune along its whole length and flowed strongly where the 1990 pipe discharged onto limestone shore rock.

By mid March 1993, evaporation and seepage through the bar had lowered water level to 2.2 m, which was still a dangerously high level for the beginning of winter (Fig 5). Above average rainfall in February to early May on a saturated catchment raised the water level to 3.3 m by 9 May. A cut was hastily made through the western dune to lower the water level without breaking the bar. However on 28-29 May, before the planned spillway could be completed, about 50 mm of rain brought river flow that raised the Inlet water level nearly half a metre in 48 hours, to 3.7 m. Water tore through the cut and opened a 70 m wide breach through the dune and beach to about 3 m below sea level, and then scoured a channel against the dune (Fig 3). The water level fell 3 m in 3 days but it was a week before the Inlet was tidal. Within six weeks the huge volume of sand and shells carried out to sea had rebuilt a wide beach to about 2.3 m above sea level and closed the Inlet.

Since the break, rainfall has been below average and Inlet water level has only briefly been above sea level. In February 1997 the Inlet was a salt pan, and when seen in April 1997 sea water was flowing into it through the eastern bar and through the beach at the breach in the western bar. The beach, at 2.5 m, was still effectively the bar and outside the line of the dune.

If the cut had not been made, flow from the 50 mm of rain of 28-29 May could have raised water level to 4.5 m and broken the eastern low bar (50 mm of rain in October 1992 caused a rise in water level of 1.4 m). The 300 mm of rain in August-October 1992 would also have broken the bar if the water level had not been so low (0.5 m) in July. There have been previous occasions when the bar was threatened by well above average rainfall and river flow without it breaking: e.g. from 1917-1920 (when it was broken artificially), in 1955 and from 1958-1960. But now, as noted above, river flow is probably considerably greater than on those occasions.

Management

Background to management

Following the floods of 1988-89, there was pressure from farmers and the Hopetoun community to prevent flooding and ensure road access from Hopetoun to the Fitzgerald River National Park. A proposal to cut the bar was deferred, and in 1990 the pipe was installed to lower the water level and reduce the risk of flooding. This did not have the capacity to cope with major floods and several proposals for the controlled release of flood water



Figure 7. Culham Inlet bar/dune area, January 1981. Scale 1:15 000. Photograph from the Department of Land Administration, Perth; Copy Licence 519/97.

at the eastern low bar were examined. The high Inlet water level (3.9 m) in October 1992 again caused extensive flooding and threatened to break the bar. Continued high water levels early in 1993 made it urgent to implement the planned controlled release of Inlet water through the western high dune before winter, but this was overtaken by river flow from the storm of May 28-29 and the water broke through.

After the break, several public meetings were held at Hopetoun to discuss the future of Culham Inlet. Everyone wanted continuous road access from Hopetoun to the Park, but inevitably there were conflicts of interest and little agreement as to the level to which Inlet water should be allowed to rise. Some low-lying paddocks are subject to flooding at 2 m and farmers did not want their land flooded, commercial fishers were concerned at the potential loss of the profitable black bream fishery (Anderson & Cribb 1994) and wanted to maintain the highest possible level, as did local residents concerned to preserve the ecosystem. The compromise reached at a public meeting in July 1993 was that the Inlet should hold as much water as possible consistent with minimal flooding of paddocks and access roads, and that the road from Hopetoun to the Park should not be closed for more than about five days once in five years (Anon 1993a). A critical water level for management is 3.5 m, above which there will be unacceptable flooding.

Management options

Five engineering measures to restore road access and manage the bar were proposed and assessed. All provided for flood water to be released at the site of the 1993 break in the bar and the roadway to be rebuilt at 4 m AHD. The first four involved rebuilding the road along its former alignment adjacent to the bar. Option 5 diverted the road inland from the bar to protect the roadway from wave action and reduce scour by flood flow (Fig 8). The five management options were;

1. Build a 120 m long floodway section of roadway at 2 m (or 2.5 m) to release flood water (Anon 1993a). This allowed for the road to be closed briefly during floods, with a probability of once in five years.
2. Rebuild the road as an effectively impermeable barrier (Anon 1993b).
3. Rebuild the road with a 40 m long sacrificial section at 3.5 m to release flood water (Anon 1993b).
4. Build a 60 m long bridge over a sacrificial section of roadway at about 3.5 m to release flood water (Anon 1993b).
5. Rebuild the road in an arc about 500 m inland from the break in the dune at 4 m (Fig 8), with a 100 m long relief floodway at 3.7 m, eleven 1.8 m diameter culverts through the road embankment at an invert level of 1 m to release flood water, and one smaller culvert at -1 m to equalise water levels between the Inlet and the pool between the roadway and the bar

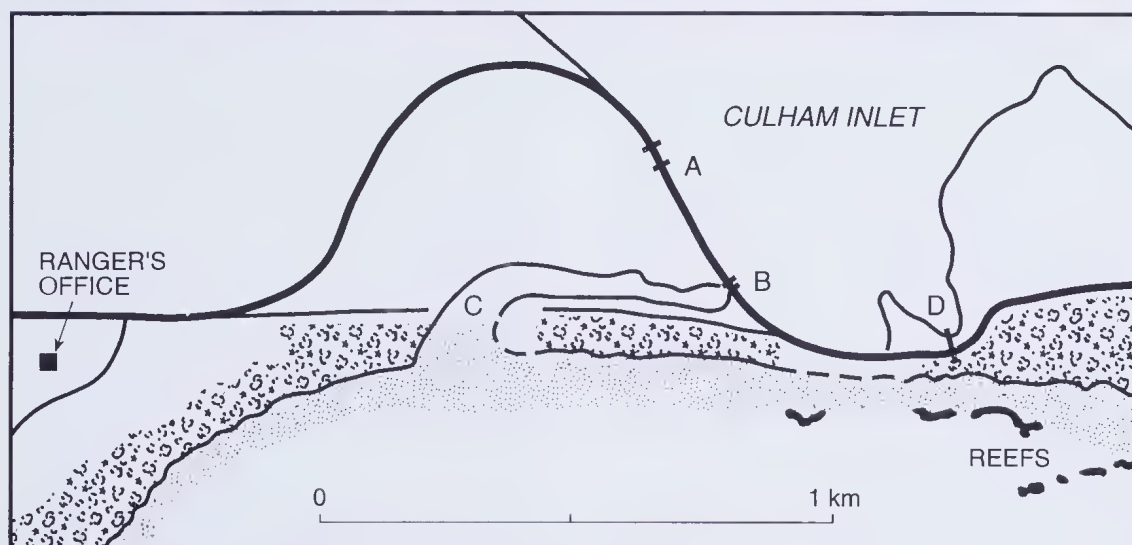


Figure 8. **Top.** Culham Inlet bar/dune area with the new road, January 1997. Sea water is seeping into the almost dry Inlet through the beach and through the scour channel and low level pipe. Photo from the Department of Land Administration; Copy Licence 530/98. **Bottom.** Explanatory diagram: A, culverts (11 at 1 m above AHD); B, culvert (1 at 1 m below AHD); C, the 1993 scour channel; D, site of the 1990 pipe.

(Anon 1995). If, as anticipated, the bar rebuilt to 3.5 m it would have to be broken when flood water reached that level.

Option 1 was not pursued when Option 4 was proposed. Options 2 and 3 were rejected because of the probability that floods would breach the road, perhaps once in 20 years, and access to the Park interrupted for long periods while it was being restored. Further study of Option 4 was not pursued because of the risk of "significant and uncontrolled failure [of the roadway] at less than acceptable frequencies" (Anon 1995). Option 5 has now been implemented and the road was opened officially on 15 April 1997.

Environmental considerations

The prime environmental objective for management should be to make Culham Inlet as healthy and productive a water body as possible and restore the Inlet to as near to its pre-1993 condition as is now practicable,

compatible with there being minimal flooding of paddocks and access roads. To achieve this the Inlet must hold as much water as possible, for as long as possible, and with a salinity less than about 70 ppt.

There is probably little river flow to the Inlet in three out of four years, mean annual evaporation is about 1500 mm, the Inlet is only 1 m deep below AHD, the water becomes >70 ppt during long periods of low river flow, and all water can be lost by evaporation. The capacity of the Inlet to accept a river flow event depends on the area of the Inlet (11 km²), the volume of flow ($\approx 11 \times 10^6$ m³ for every 1 m depth), the initial water level, and the height of the retaining barrier. The volume and timing of river flow depend on rainfall and the moisture content and compaction of the catchment soils. Rainfall and soil moisture are unpredictable and so too must be the volume and frequency of river flow, while the depth and salinity of water retained after flood flow will depend on the height of the barrier. On past experience, the

combination of events which produced the high water levels of 1989, 1992 and 1993 might be expected to recur once in about fifty years. However, river flow may have at least doubled as the result of catchment clearing during the last 30 years, and the previous 50-year probability of a 3.5 m high bar breaking may now be a 20 to 30-year probability, and a 2.5 m bar breaking every five to seven years.

The potential for management to achieve the above environmental objective for Culham Inlet (i.e. with as much water as possible for as long as possible and the salinity less than about 70 ppt) will depend on the height of the retaining barrier and how often it breaks.

Option 1 would retain flood water to the level of the floodway (2 m or 2.5 m) with a maximum depth of 3 to 3.5 m of water. The Inlet would again be a closed salt lake, but the water would become hypersaline and all water dry up more often than in the past. Options 2, 3 and 4 have the potential to retain water to 3.5 m (Option 2 to 4 m) with the capacity to return the Inlet close to its pre-1993 condition until the water level reaches 3.5 m and the road/bar is breached. All Inlet water would then be lost down to sea level, the Inlet would be briefly an estuary as in May 1993, and would only revert to its previous condition after the barrier was rebuilt.

The Option 5 road and pipes are now in place. However four years after the bar was breached, the beach was still effectively the bar; it was at 2.5 m and still seaward of the dune line. In this situation it can be breached (either from the Inlet or by wave action) so frequently that a stable bar is unlikely to rebuild higher on the dune line naturally. When the bar breaks all water will be lost down to 1 m and leave only 2 m depth of water, water that can become hypersaline and dry up. The Option 5 proposal envisaged the bar rebuilding to 3.5 m on the dune line (Anon 1995) and at that height it would retain water to a depth of 4.5 m and Culham Inlet would have the potential to be a healthy and productive a waterbody again — while the bar held.

Discussion

Culham Inlet was an estuary until about 3500 years ago, but probably for several hundred years it has been a coastal salt lake with a high sea bar that last broke naturally in 1845. The water level varied from -1 m to 4 m AHD (0 m to 5 m deep) and salinity from 10 ppt to brine. In 1989 and 1992 river flow raised water levels in the Inlet so high that the stability of the bar was threatened, and the road along it was impassable. In May 1993 the water level was already so high that the Inlet no longer had the capacity to accept that month's river flow, and the bar broke. Following the break, the priority for management was to ensure road access to the National Park and limit paddock flooding. The road has been rebuilt; but what is the future of the Culham Inlet ecosystem? Can it be a healthy and productive environment again?

The health and productivity of Culham Inlet depend mainly on the depth and salinity of the water. Depth and salinity are dictated by rainfall and river flow, and the height of any retaining barrier and the frequency with which it breaks. It was anticipated that the bar would

rebuild to 3.5 m at which height a stable bar on the dune line could be expected break with a frequency of only once in 20 to 30 years. But in May 1997 the beach was still the bar, at 2.5 m and seaward of the dune line, and it can be expected to break relatively frequently, perhaps once every five to seven years, and with such frequent breaks it is unlikely to rebuild higher naturally. When the bar breaks, the water will be lost down to 1 m, only 2 m deep, and will become hypersaline and dry up more often than in the past — considerably more frequently with a 2.5 m beach/bar than with a 3.5 m stable bar that can retain water to a depth of 4.5 m. The bar could be rebuilt to 3.5 m from the excess of sand now on the wide beach; there would be short-term flooding of farm land before the bar broke, but this would seem to be a small price to pay for Culham Inlet to have the potential to be as productive an ecosystem as is now possible.

The combination of well above average rainfall in 1992, especially in the cleared upper catchment, the saturated catchment, the high Inlet water level and the high rainfall of May 1993 may have been unusual for the time of year, but the 50 mm of rain of 28-29 May could be expected to recur once in 2.5 years. It was the large volume of river flow from that rain that broke the bar; it was beyond the available capacity of the 11 km² Culham Inlet to accept at that time. The nearby Jerdacuttup Lakes (Fig 1) has three times the area to absorb flow and would not have been threatened. The last time the Culham bar is known to have been threatened was in 1955 when only about 10% of the catchment was cleared, but now with about 40% cleared the river flows of 1992-93 were probably much greater. Coastal lakes and estuaries in the south coast low rainfall area are the receiving waters for river flow from catchments that have been extensively cleared since the 1960s. The bars of two 'normally closed' estuaries, Beaufort Inlet and Stokes Inlet, have broken more frequently following clearing in the catchments; and flood flow has increased sediment transport to their shallow basins (Hodgkin & Clark 1988, 1989). Landcare groups are now implementing management measures in the catchments to reverse the rising water tables and prevent salinisation, and it is to be hoped that these measures will in time reduce runoff and river flow, and soil erosion and sediment transport to the coastal lakes and estuaries.

Acknowledgments: Assistance from staff of the Department of Environmental Protection and the Marine and Harbours Branch of the Department of Transport and access to their files is acknowledged. I am grateful to R Cooper for permission to use his data on water levels in Culham Inlet, and to M Cliff for information on fish catches. W S Andrew, R Clark, and R C J Lenanton have kindly read and discussed drafts of the paper. The support of members of the Hopetoun community is greatly appreciated, especially that of H and R Taylor.

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Pre-contact human skeletal remains from Useless Loop, Western Australia

N G Jablonski¹ & S Bowdler²

¹ Department of Anthropology, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118-4599 USA email: njablonski@calacademy.org

² Centre for Archaeology, Department of Anthropology, The University of Western Australia, Nedlands, WA 6907 email: sbowdler@cyllene.uwa.edu.au

Manuscript received November 1996; accepted July 1997

Abstract

A human skull found in 1992 near Useless Loop, Western Australia is described here as being that of a pre-European contact Aboriginal Australian. The skull was that of a gracile male of approximately 50 years of age at the time of death. Teeth recovered with the skull showed heavy wear, and lesions in the alveolar bone of the jaws suggested that the individual possibly suffered from periodontal disease and, probably, at least one painful abscess at the time of death. The morphology of the individual was similar to that of other, contemporary populations of Aboriginal people from the central region of Western Australia.

Determination of the absolute age of a sample of cranial bone by accelerator mass spectrometry yielded a probable age of 2730 ± 400 yr bp. This find therefore represents one of a very few sets of pre-European contact human remains in Western Australia to have been recovered from a known location.

Introduction

Archaeological research in the region of Shark Bay, Western Australia, over the last ten years has revealed a thirty thousand year history of occupation (Bowdler 1990a,b,c, 1995). The evidence has consisted primarily of stone artefacts and food refuse, collected or excavated from open midden and rock shelter sites. Few pre-European human remains were known from the region, and none have ever been excavated from a primary context, or securely dated. The find reported here, while not completely satisfactory in terms of depositional context, at least represents pre-European human skeletal remains from a known location.

In October 1992, a human cranium was found on the track north of the township of Useless Loop which had been graded four months previously (Bowdler, *unpublished observations*). It was presumed that the cranium had been disturbed from its original resting place by the grader, and could have been moved by up to 400 m. The spot of the find was marked by a wooden stake. The skull was found half-buried in a grader windrow on the side of the track. The spot is about 10-15 m above sea level, on a fairly narrow neck of the Prong, and no more than 100 m from the coast in a straight line. It is, in fact, the sort of place where it would not be unexpected to find a prehistoric site, an open midden scatter of the kind common in this region (Bowdler 1990a,b). On careful examination near the find, a human incisor was found which, from its state of wear, appeared to be that of a prehistoric Australian Aboriginal person. Fourteen meters to the south, also on the side of the road, were found a chalcedony flake and a piece of baler shell. On

the track and its sides, about 50-100 m to the south, was evidence of a scattered midden site, consisting of *Terebralia*, baler, *Turbo*, and other marine shells. The accumulation was not very dense, but was reasonably evident. A few calcareous flakes were noted also. The soil was a light-coloured dune sand; no darker horizon was evident anywhere. Further cranial remains, including the mandible, were recovered approximately six months later within 100 m of the original find. Because the second set of remains matched exactly the expected description of the missing portions of the cranium and mandible, the two sets were assumed to have been originally associated.

We describe here these newly discovered cranial remains and compare them with those of others known from the area, and more widely in Australia. The age is estimated and the significance of the find is discussed. In accord with the wishes of the Aboriginal people in Denham, the skull was re-interred near the spot of its discovery after it had been studied.

Materials and Methods

Morphometry

The cranium (hereafter designated the ULHK cranium) was examined and measured at Useless Loop and again at the Department of Anthropology, University of Western Australia. A standard battery of anthropometric measurements were made on the ULHK cranium for comparison with measurements for other modern human populations reported by Howells (1973, 1989). The cranium was measured using digital calipers, standard spreading calipers, and coordinate calipers. The average value of three measurement trials, rounded to the nearest

millimeter, is presented in this report. Complete descriptions of the measurements can be found in Howells (1973). An estimate of the cranial capacity of the cranium was made by measuring the volume of the sand that filled the endocranial cavity, using a beaker (to $\pm 50 \text{ cm}^3$).

The computer software program CRANID (Wright, 1989/1992) for the automated comparison of cranial measurements was used to assess the affinities of the ULHK cranium. This program permits comparison of the dimensions of any unknown human cranium with the dimensions of 2524 female and male crania from around the world based on measurements reported by Howells (1973, 1989). The IDCAN2 routine of CRANID was used to analyse the average values of the measurements. The first analysis in this routine provides a catalogue of the 50 nearest neighbors of the cranium in question. The second analysis in this routine (the K-means cluster analysis) indicates that the composition of the group that is closest in shape to the cranium in question.

Dating

Two dating strategies were employed. First, a radiocarbon date was obtained for marine shell remains (*Terebralia* sp) gathered from the nearby midden site. It seemed a reasonable assumption that the skull could have been associated with the prehistoric site. Second, following consultation with Aboriginal people in Denham, a piece of bone from the nasal area of the skull itself was submitted for radiocarbon dating to the Quaternary Dating Research Centre at the Australian National University. Accelerator mass spectrometry radiocarbon dating with the 14UD accelerator of the Research School of Physical Sciences and Engineering was conducted by J Head. Two fractions, bone apatite and collagen, were dated separately.

Results

Description of the remains

The human skeletal remains consisted of a single human cranium and mandible designated ULHK for purposes of this report. Selected standard views of the ULHK remains are provided in Figures 1-4.

Nearly all elements of the cranium were recovered during the course of the investigation. Because the mandible and fragments of the upper facial skeleton were recovered several months after the cranium had been returned to Useless Loop, no attempt was made to reconstruct the complete skull. The elements of the upper facial skeleton that were separated from the main mass were as follows; the maxilla (except orbital process), the pterygoid plates of the sphenoid, the zygomatic bone and the zygomatic process of the temporal bone. The damage to the cranium that separated the bones of the upper right facial skeleton occurred *post mortem*, and was almost certainly caused by the road grader which disintegrated the cranium. The supraciliary ridge on the right side has been punctured *post mortem*, revealing a large frontal sinus (Fig 1). The puncture hole was almost certainly produced by the action of the road grader. No fractures were evident.

A comparison of the measurements of ULHK cranium with those of other samples from Western Australia



Figure 1. ULHK cranium, *norma frontalis*. Note damage to upper facial skeleton and supraciliary ridge on right side. Approximately one-half actual size.



Figure 2. ULHK cranium, *norma basalis*. Note the small hole in the alveolar bone of the maxilla in the molar region possibly resulting from a dental infection. Approximately one-half actual size.



Figure 3. ULHK cranium, *norma lateralis* (left). Note bleaching of bone on top of calvaria and in the occipital region. Approximately one-half actual size.

(Table 1) indicates that the Useless Loop specimen was very similar in size to other males from the state, and especially to those from the central region of Western Australia (defined by Margetts & Freedman (1977) as around Port Hedland, North West Cape, Shark Bay and Cue).

Several teeth were associated with the skull, but only three were measurable (Table 2). In the upper dentition, only the heavily worn stump of the right upper third molar was found in its alveolus. The heavily worn left upper central incisor and left canine were recovered at the site by sieving. The alveoli of the upper left central incisor, lateral incisor, canine, and first premolar were well preserved and clearly held teeth at the time of death. The alveoli of the upper left first molar and third molar were shallow and may have held teeth at death, but the alveolus of the second molar appears to have been resorbed long before death. A small natural opening in the alveolar bone in the second to third molar region (Fig 2) communicated with the antrum of the maxillary sinus; this suggests that one of those teeth may have been abscessed at the time of death or that an oro-antral fistula had occurred following the loss of an infected molar. In one of the fragments of the right facial skeleton that was recovered, a similar lesion was found in the floor of the maxillary sinus above the upper third molar.

The mandible was complete and did not show signs of dental abscesses or excessive periodontal disease. Preserved on the right side of the mandible were the alveoli of the lateral incisor, the canine, third premolar, the fourth premolar, and the first molar. Four heavily worn teeth were recovered on the left side of the mandible; the canine, third premolar, fourth premolar (stump only, worn to the cervix) and third molar. The alveoli of the first and second molars were also preserved. Resorbed alveoli indicated that several teeth had been lost *ante*

mortem on the left side, the central and lateral incisors; on the right side, the central incisor, the first or second molar, and the third molar had been lost.

Judging from the advanced state of wear of the teeth and the absence and/or diseased state of the molar teeth, the individual's ability to chew was no doubt compromised.

The cranium was uniformly medium brown in colour except for two areas, on the top of the calvaria and on the left parietal and occipital bones (Figs 1, 3, 4), that appear to have been bleached by recent exposure to the

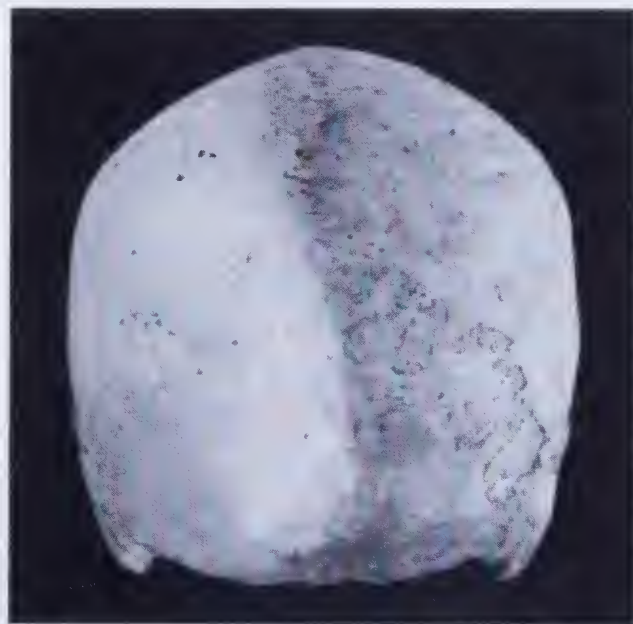


Figure 4. ULHK cranium, posterior view. Approximately one-half actual size.

Table 1

Measurements (in mm) of the ULHK cranium compared to those of the following other modern human cranial samples; 1) the mean and range of Western Australian Aboriginal male and female crania [WA-M and WA-F] reported by Margetts & Freedman (1977); 2) the mean for central Western Australian male crania [CWA-M] reported by Margetts & Freedman (1977); 3) and the centroid of the distribution of populations of living *Homo sapiens* measured by Howells (1973, 1989). The standard abbreviations for the measurements are as follows; glabello-occipital length (GOL); nasio-occipital length (NOL); basion-nasion length (BNL); basion-bregma height (BBH); maximum cranial breadth (XCB); maximum frontal breadth (XFB); biauricular breadth (AUB); biasterionic breadth (ASB); basion-prosthion breadth (BPL); nasion-prosthion height (NPH); nasal height (NLH); orbital height [left] (OBH); orbital breadth [left] (OBB); bijugal breadth (JUB); nasal breadth (NLB); palate breadth (MAB); bimaxillary breadth (ZMB); zygomaxillary subtense (SSS); bifrontal breadth (FMB); nasio-frontal subtense (NAS); biorbital breadth (EKB); interorbital breadth (DKB); cheek height (WMH); nasion-bregma chord (FRC); nasion-bregma subtense (FRS); bregma-lambda chord (PAC); bregma-lambda subtense (PAS); lambda-opisthion chord (OCC); and lambda-opisthion subtense (OCS). The values from Margetts & Freedman (1977) have been rounded to the nearest mm.

	ULHK	WA-M mean (range)	WA-F mean (range)	CWA-M mean	<i>Homo sapiens</i> centroid
GOL	192	187 (169-202)	177 (163-191)	188	179
NOL	187	-	-	-	177
BNL	100	101 (91-116)	97 (76-129)	101	99
BBH	133	131 (121-144)	128 (120-143)	130	132
XCB	139	131 (117-143)	130 (120-143)	131	137
XFB	110	-	-	-	113
AUB	122	118 (106-131)	113 (104-127)	-	121
ASB	110	107 (97-117)	104 (94-122)	-	107
BPL	98	103 (95-119)	97 (62-107)	104	98
NPH	73	69 (60-87)	65 (53-75)	70	66
NLH	52	49 (42-77)	46 (40-59)	51	50
OBH	33	33 (28-44)	32 (26-38)	34	34
OBB	40	40 (30-44)	32 (26-38)	40	39
JUB	114*	118 (105-134)	109 (98-125)	-	115
NLB	29*	28 (23-38)	26 (21-30)	28	26
MAB	29*	-	-	-	63
ZMB	96*	92 (80-107)	88 (80-103)	93	95
SSS	20	-	-	-	23
FMB	103	101 (86-110)	97 (91-111)	-	97
NAS	20	-	-	-	16
EKB	100	100 (93-110)	95 (89-101)	-	97
DKB	24	22 (18-28)	20 (17-23)	22	21
WMH	24	-	-	-	23
FRC	108	112 (99-124)	106 (95-116)	-	109
FRS	23	25 (20-31)	26 (21-34)	-	25
PAC	112	116 (104-128)	109 (97-126)	-	111
PAS	23	-	-	-	24
OCC	101	94 (82-105)	95 (85-108)	-	96
OCS	33	-	-	-	28

*denotes a measurement made on the assumption of bilateral symmetry

Table 2

Measurements (mm) of the three measurable teeth from the ULHK remains, compared with mean and range (in brackets) of Western Australian Aboriginal males and females reported by Freedman & Lofgren (1981). Mesiodistal (MD) and buccolingual (BL) dimensions are given.

Tooth	ULHK	ULHK	WA Male		WA Female	
	MD	BL	MD	BL	MD	BL
Upper left lateral incisor	6.52	7.45	7.24 (5.8-8.6)	7.03 (5.8-7.9)	7.10 (5.2-8.3)	6.67 (5.6-7.8)
Upper left canine	7.19	9.67	8.01 (6.8-9.5)	9.18 (7.6-10.1)	7.81 (7.4-8.4)	8.44 (7.6-9.1)
Lower left canine	7.50	11.10	7.28 (6.0-8.4)	8.67 (7.5-9.8)	6.91 (6.2-7.6)	7.79 (7.2-8.7)

sun. The cranial cavity was filled with dry, compact sand, and the rootlets of some plants were found adhering to the endocranial surface, to the orbits and to the outside of the base of the skull. No soft tissues or hair were found. The bone of the cranium and mandible was well preserved and quite sturdy, but there was no indication that fossilization had begun. Relatively little mineral content had been lost during its period of interment, a condition that would have been consistent with burial in a well-drained location. The length of time that the cranium had been in the ground could not be accurately estimated by simple visual examination. The volume of the endocranial cavity was approximately $1450 \text{ ml} \pm 50 \text{ ml}$, which is within the range for modern human males.

Estimation of age at death

Sutural fusion and obliteration on the ectocranial surface of the cranium was advanced and the same appears to have been true on the endocranial surface, as far as could be seen. The central parts of the coronal suture (at bregma), the rostral half of the sagittal suture and the central part of the lambdoidal suture were nearly completely obliterated. Estimation of age at death from the skeletal remains of adults is fraught with uncertainties and is particularly difficult in cases such as this where no postcranial remains (including the potentially useful pubic symphysis) have been recovered. On the basis of the status of the cranial sutures and dentition, the minimum age of this individual is judged to have been 50 years (estimated range 45–55 yr). The sturdiness of the cranial bones and the absence of marked thinning of these bones would further suggest that the individual was not of an advanced age.

Sex of the individual

At the time that the cranium was first examined, the first author judged it to be female because the cranium bore relatively gracile muscular markings despite being sturdily built. Further detailed study, however, suggested that the skull was almost certainly that of a male, after examination of other cranial remains of Aboriginal individuals at the Western Australian Museum (Perth) and the Natural History Museum (London) and after following the methods of sex determination described by Larnach & Freedman (1964). Unfortunately, because no further skeletal remains were found with the skull, confirmation of sex using elements of the postcranium was not possible.

Racial affinity

The presence of a suite of several morphological features of the cranium clearly indicates that the individual was an Aboriginal Australian. These features include the marked development of the supraorbital region, a low forehead rising gently to bregma, a broad interorbital region, rectangular orbits, short nasal bones, a large nasal opening, a calvaria showing a "gabled" or "barn-roof" outline (Fig 4), and the presence of an occipital "bun" (Fig 3). These results of visual inspection of the cranium were reinforced by the quantitative analysis.

Unusual features

In the lambdoidal suture were found six sutural (wormian) bones or Ossa Incae, two of which can be

clearly seen in Fig 3. Such bones represent accessory centres of ossification and are present as common variations in human crania world-wide.

The cranial base was slightly asymmetrical. The right occipital condyle bore a posterolateral extension not seen in its antimer (Fig 2) and the space occupied by the jugular bulb was about 50% larger on the right than on the left. Such asymmetries are common to all human groups and probably had no effects on the individual during life.

Quantitative morphological analysis

The measurements of the ULHK cranium were compared to those of other Aboriginal crania from Western Australia as compiled by Margetts & Freedman (1977) and to the centroid of the distribution of Howells' (1973, 1989) entire sample of crania from modern human groups. In most cases, the raw measurements of the cranium ULHK fit comfortably within the range for male crania from Western Australian Aborigines.

The first analysis of the IDCRAN2 procedure indicated 50 crania from Howells' sample that were most similar to the ULHK cranium (note that the comparative sample of Howells' on which CRANID is based includes measurements from southern and eastern, but not western Australian Aboriginal skulls). This list revealed that the ULHK cranium was similar to that of many diverse human groups; the single nearest "morphological neighbor" of the ULHK cranium was a female cranium from the Tolai population in New Britain but this should not be construed to indicate that the ULHK cranium was of an individual from New Britain. This similarity is not surprising in light of the recognized morphological similarities of Melanesian and Aboriginal Australian populations (Howells 1973, 1989). The K-means cluster analysis indicated clearly that the groups that best matched the ULHK cranium were South Australian and Tasmanian Aborigines, although the cranium also showed strong affinities with groups from New Britain and East Africa.

The results of the quantitative morphological analysis support the visual assessment presented in the previous section that the ULHK skull was that of a male Australian Aboriginal.

Absolute age of the ULHK remains

Dating of the marine shell from the midden site gave an age of $7400 \pm 70 \text{ bp}$, which if corrected for the oceanic reservoir effect produces a date of $6950 \pm 70 \text{ bp}$. This date is entirely consistent with many other midden sites in the Shark Bay region with *Terebralia* shells. We cannot, however, assume that the skull was in fact associated with this site.

With respect to bone from the skull itself, the apatite fraction gave an age of $2730 \pm 400 \text{ yr bp}$, and the collagen fraction produced an age of $750 \pm 250 \text{ yr bp}$. The older of the two bone dates would be generally considered the better date because most contamination comes from younger sources of carbon (J Head, Australian National University, *personal communication*).

The shell-derived date is, technically speaking, a more reliable date for the event which it dates, which is the gathering of these particular molluscs. It also fits well

with other dates from these shell species collected and excavated from shell midden sites in the Shark Bay region. The bone date must be preferred, despite its technical imprecision, as a date for the death of the individual from which the bone was derived.

Discussion

The results of visual analysis of the ULHK cranium and analysis of the measurements of the cranium using CRANID indicate that the ULHK skull was that of a male Aboriginal Australian, who was probably about 50 years old at the time of death. The state of preservation of the bone of the cranium was generally good, and all the damage sustained to the cranium on the right side of the facial skeleton and right supraciliary ridge was consistent with damage caused by the road grader which unearthed the cranium. The ULHK cranium represented an individual who suffered from extreme dental wear and reasonably serious dental disease near the time of death.

Measurements of the ULHK cranium were found to be very similar to those of other samples of male crania from Western Australia. In their comparative study of a large series of modern Aboriginal crania from Western Australia and coastal New South Wales, Margetts & Freedman (1977) noted progressive morphometric separation between equivalent parts of the two states. That is, greater similarities between the northern populations, and progressively fewer between the central and southern populations, were found. This result, they indicated, was suggestive of a north to south migration down the east and west coasts. An alternative explanation can also be offered. The greater similarities between the northern populations of eastern and western Australia may have been due to greater genetic interchange between these populations because of fewer major ecogeographical barriers between them. The increasingly greater differences between central and southern populations may have been due to a greatly reduced chance of genetic interchange between the populations resulting from greater distances and more severe ecological barriers separating them.

The ULHK skull appears to represent an individual who was buried at the top of a hill in such a way that the skull came to protrude from the side of the track cut through the crest of the dune. It was then scooped up by the grader and redeposited at the spot of the find in the track. It is likely that the postcranial remains remain *in situ* in the side of the track. Recommendations made in an original (Bowdler, 1992, *unpublished*) report to the former Aboriginal Sites Department (Western Australian Government, Perth) included the future possibility of finding further skeletal materials at the same site.

The ULHK skull was found close to a midden dated to about 7000 yr bp, but the skull itself appears to be around 2700 or possibly even 750 yr old. Whichever date is more accurate, the skull clearly predates the arrival of Europeans in Western Australia. Illustrated descriptions of such finds are rare. The ULHK skull represents an important example of central Western Australian Aboriginal morphology that contributes to our understanding of human variability as it existed in Australia during the Holocene, prior to European settlement.

Acknowledgements: SB would like to thank the members of the Yagdallah Club in Denham and particularly S Gosper, for their help and for granting permission to publish the findings of this study. J Head is thanked for expediting the AMS date, and S McGann for assistance in the field. People at Useless Loop were particularly helpful and friendly, especially G and S Privett, R O'Keefe and H Bielawski. NGJ would like to thank M Lofgren (Western Australian Museum, Perth) and C Stringer (Natural History Museum, London) for access to skeletal remains in their care.

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Status of a shallow seagrass system, Geographe Bay, south-western Australia

K McMahon¹, E Young^{1,2}, S Montgomery¹, J Cosgrove¹, J Wilshaw¹ & D I Walker^{1a}

¹Department of Botany, The University of Western Australia, Nedlands, WA 6907

²Current address: DEEB, Monash University, Clayton VIC 3168

^aemail: diwalker@cyllene.uwa.edu.au

Manuscript received December 1996; accepted March 1997

Abstract

Geographe Bay, southwestern Australia, is a shallow open embayment with sandy substrata dominated by the seagrass *Posidonia sinuosa*, which has greater than 60% cover of the bay. The surrounding agricultural catchments are sandy and low-lying, with extensive drains contributing anthropogenic nutrients (255 tonnes of N and 34 tonnes of P seasonally) to Geographe Bay. Potential for eutrophication of this system and the subsequent effects on the biota, particularly the health of seagrass communities, has been of concern by local residents. This study documented physical parameters in the water column and the distribution and status of the benthic biota from 1993 to 1995. There were seasonal changes in water temperature (ranging between 14.8 °C in winter to 21.6 °C in summer), and irradiance (ranging between 0 in winter to 850 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in summer). These changes followed expected seasonal patterns in a mediterranean climate. Above-ground biomass of the dominant seagrass *Posidonia sinuosa* (115 to 470 g m^{-2}) was similar to that reported for unpolluted systems in southern Australia, as was epiphyte load (0.1 to 26 g m^{-2}). Geographe Bay showed few symptoms of eutrophication despite seasonal increases in nutrient loads

Introduction

Geographe Bay is a 100 km wide north-facing embayment, situated between Cape Bouvard and Cape Naturaliste, on the south western coast of Australia (Fig 1). It is a relatively protected bay with a gentle sloping bathymetry (2 m km^{-1}). A Holocene sediment veneer overlies Pleistocene limestones and clays (Paul & Searle 1978). The shallow subtidal region (2-14 m) is characterised by sandy substrata interspersed with limestone pavements and reef. There are extensive beds of seagrass *Posidonia sinuosa* Cambridge & Kuo, with greater than 60% coverage throughout the bay. *Amphibolis antarctica* (Labillardiere) Sonder *et* Ascherson *ex* Ascherson, often occurs on the periphery of *P. sinuosa* meadows and limestone pavements (Walker *et al.* 1987).

Land bordering Geographe Bay has been cleared extensively for agriculture over the last 150 years. A network of drains was developed to facilitate agricultural and urban development (Fig 1). Cattle farming with lesser amounts of sheep farming and potato and lucerne crops, are the predominant agricultural practices. The soils in the district have poor nutrient retention capacities and are highly leached with low ambient nutrient concentrations (McComb & Davis 1993). The establishment of agriculture has relied extensively on the addition of nutrients, especially trace elements, phosphatic and nitrogenous fertilisers (McComb & Davis 1993). Much phosphorus is lost to drainage from leaching sandy soils (Hodgkin & Hamilton 1993). This results in an increase in nutrients draining from the Geographe Bay catchment. These have been calculated as an annual total of 255

tonnes of nitrogen and 34 tonnes of phosphorus (Holmes 1995).

Increases in nutrient concentrations above a particular level in a system often result in eutrophication (Stirn 1994). Detrimental effects on coastal systems over-enriched with nutrients have occurred worldwide (Nixon 1993) and can be identified as symptoms of eutrophication. These include biological factors such as;

- the presence of phytoplankton and macroalgal blooms especially an increase in frequency, duration and extent of the blooms (Lukatelich & McComb 1989; Malone 1991);
- high algal epiphyte biomass often measured as epiphyte biomass to seagrass leaf biomass;
- absence of or low biomass of benthic macrophytes (Cambridge *et al.* 1986; Silberstein *et al.* 1986; Neverauskas 1987, 1988);
- shifts in species composition (Lukatelich & McComb 1989);
- decrease in diversity of organisms (Walker *et al.* 1991); and
- increase in diseases of fish and water fowl (Kemp *et al.* 1984);

and physical factors such as;

- high light attenuation coefficient; and
- low dissolved oxygen concentrations (Dubravko *et al.* 1993).

With nutrient enrichment, phytoplankton can rapidly increase biomass and bloom (Ryther & Dunstan 1971). Chlorophyll *a* is a relative estimate of phytoplankton

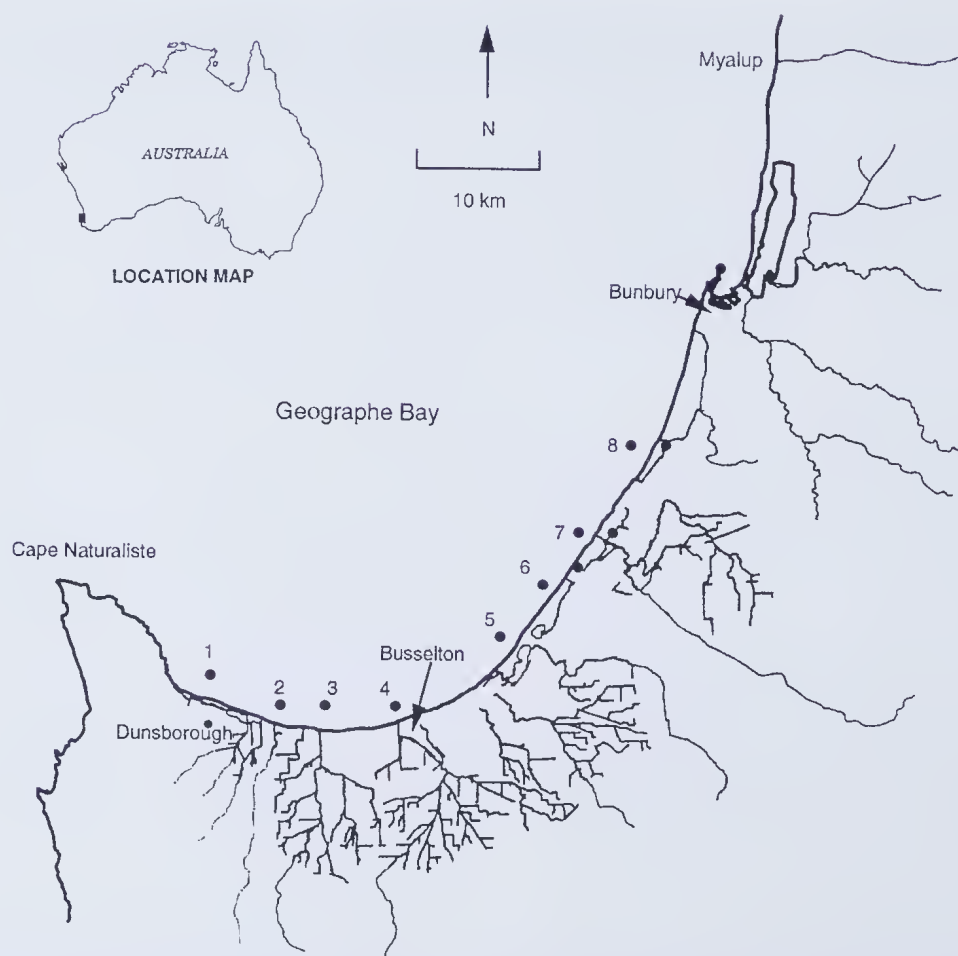


Figure 1. Map of Geographe Bay showing the location of the study sites; 1, Dunsborough; 2, Toby's drain; 3, Buayanup drain; 4, Vasse-Diversion drain; 5, Vasse-Wonnerup Estuary; 6, Forrest Beach; 7, Capel River; 8, 5 Mile Brook diversion.

biomass (Round 1981). Concentrations greater than $1 \mu\text{g l}^{-1}$ are higher than background levels in the oligotrophic, temperate waters of south Western Australia, and indicate blooms of phytoplankton (Anon 1993). Cyanobacteria may also bloom under conditions of nutrient enrichment (Hallegraeff 1992). Under nitrogen-limited conditions with an adequate phosphorus supply, cyanobacteria can proliferate due to their ability to fix and supply their own nitrogen requirements (Round 1981).

Biomass of opportunistic epiphytes may be boosted under conditions of nutrient enrichment, if other variables are favourable for growth (Pickering *et al.* 1993). The epiphyte to leaf biomass ratio (E/L) is a indicator of excessive epiphyte loads on seagrasses (Penhale & Smith 1977). Values of E/L greater than 0.3 for *P. sinuosa* indicate excessive epiphyte biomass with a deleterious shading effect on the seagrass (Neverauskas 1987).

The presence of submerged aquatic vegetation can be an indicator of water quality (adequate light penetration) and nutrient status *i.e.* low nutrient concentrations (Walker & McComb 1992; Dennison *et al.* 1993). In eutrophic systems where light is often reduced for extended periods, there may be decreases in the biomass of benthic macrophytes (Neverauskas 1988; Sand-Jensen & Borum 1991). The changes in seagrass biomass can be an indicator of the extent of eutrophication (Hillman *et al.* 1989). For the seagrass *Posidonia sinuosa* in a

monospecific meadow down to 4 m deep, biomass ranges between 250 and 500 g m^{-2} (Hillman & Morrison 1994). A decrease from this range may indicate that seagrasses growing in the same depth and under similar conditions are under stress (Neverauskas 1987).

There have been recent concerns about the health of the Geographe Bay system. Losses of seagrass cover in some nearshore areas were documented in the 1970s (Conacher 1993), but the study showed some indication of subsequent recovery. Anecdotal evidence of macroalgal blooms in summer are of concern as potential symptoms of eutrophication. The aim of this study was to document physical and biological conditions in Geographe Bay. Physical profiles of light, temperature and salinity were recorded. Biological measures of seagrass biomass, algal epiphyte load, chlorophyll *a* concentration, the presence or absence of cyanobacterial and diatom aggregations and the presence or absence of seagrass wrack were taken. These were interpreted to assess whether there were any symptoms of eutrophication in Geographe Bay.

Methods

Geographe Bay has a temperate, mediterranean type climate, characterised by warm, dry summers and cool, wet winters (Walter 1979). The annual rainfall is 800 mm

a year, with 85% of the rain falling between May and October (Fahrner & Pattiaratchi 1995). In summer the winds are generally easterly in the morning at speeds of 5 m s^{-1} with a south-southwesterly sea breeze in the afternoon, with speeds up to 15 m s^{-1} . Winter weather patterns are dominated by the passage of westerly cold fronts associated with low pressure systems which cross the coast every 7 to 10 days. These result in strong, sustained west to north-westerlies of up to 15 m s^{-1} . An average of 15 days of winter storms occur every year (Fahrner & Pattiaratchi 1995).

Water movement in Geographe Bay is mainly wind driven, as the tidal range is small, generally less than 1 m. Fahrner & Pattiaratchi (1995) predicted a predominantly northerly transport of water along the perimeter of the bay from Cape Naturaliste to Myalup in westerly, south-westerly and southerly winds. South-easterly winds result in the offshore transport of water and easterly winds, in the offshore transport of water in a south-westerly direction. North-westerly winds would result in the onshore transport of water with weak and variable currents. The average flushing time off Busselton is predicted as 3 to 5 days for easterly, southerly and south westerly winds. Longer flushing times, up to 14 days, occur when south-easterly and north-westerly winds dominate (Fahrner & Pattiaratchi 1995). In recent years, a cold current (the 'Capes Current') has been documented in the south west of Western Australia (A Pearce & C Pattiaratchi, *pers comm*); it originates on the western side of Cape Naturaliste, impinges on the nearshore of Geographe Bay, and moves northward, along the coast-line to Perth.

Eight sites were chosen to survey physical and biological conditions in nearshore Geographe Bay (Fig 1). Six were potential impact sites, off-shore from drainage systems (Toby's drain, $33^\circ 37.797' \text{ S } 115^\circ 10.794' \text{ E}$; Buayanup drain, $33^\circ 38.531' \text{ S } 115^\circ 14.933' \text{ E}$; Vasse-Diversion drain, $33^\circ 38.339' \text{ S } 115^\circ 19.303' \text{ E}$; Vasse-Wonnerup Estuary, $33^\circ 36.116' \text{ S } 115^\circ 25.401' \text{ E}$; Capel River, $33^\circ 30.194' \text{ S } 115^\circ 31.362' \text{ E}$; 5 Mile Brook Diversion, $33^\circ 27.572' \text{ S } 115^\circ 33.593' \text{ E}$) and two were used as reference sites with no direct terrestrial run-off (Dunsborough, $33^\circ 36.425' \text{ S } 115^\circ 07.112' \text{ E}$; Forrest Beach, $33^\circ 34.265' \text{ S } 115^\circ 26.783' \text{ E}$). Over the summers of 1993/1994 and 1994/1995, surveys were undertaken every fortnight. In April, July and September 1994, four sites were sampled more intensively (Buayanup drain, Vasse Diversion drain, Vasse-Wonnerup Estuary and Dunsborough). In July 1994, only Dunsborough and Vasse-Wonnerup Estuary were sampled due to rough weather conditions.

Each site was located in 5 m of water, approximately 500 m from shore, in the middle of a seagrass bed. At each site, light and temperature profiles were recorded, and benthic communities surveyed. In July 1994, benthic communities were not surveyed due to turbid conditions. The information for the eight sites sampled intensively over the summers was used as general habitat descriptions. The data from the four sites studied over the whole year were used to compare physical and biological conditions.

Light and temperature

Temperature ($^\circ\text{C}$) and light intensity ($\mu\text{mol m}^{-2} \text{ s}^{-1}$) were measured with a Hamon Yeokal temperature/salinity

bridge and a Licor light meter with an underwater sensor. A vertical profile was carried out at 1 m intervals from the bottom to 1 m from the surface, then at 0.5 and 0.1 m from the surface. Light measurements were used to calculate a vertical light attenuation coefficient as the slope of the line between log of light and depth (Kirk 1994). Secchi disk depth (Z_{sd}) readings were made and attenuation coefficients were then calculated using the formula $K_d = 1.44/Z_{sd}$, where K_d is the attenuation coefficient (Kirk 1994).

Benthic communities

A 300 m equilateral triangular transect (100 m each side) was swum with SCUBA at each site to document benthic communities and physical features. Observations were made at 10 m intervals along the transect. The type of substratum was recorded as sand, low pavement rock or high rock and the percentage cover of benthic biota was noted. This percentage cover was a visual estimate of the amount of substratum covered by seagrass and/or macroalgae over a 10 m distance and the value was estimated at 1 m distance above the transect, taking into consideration 1 m either side of the transect. Macroalgae were collected for identification. The presence or absence of monospecific diatom and blue-green aggregations and their relative abundances along the transect were also noted. The number of times each group was present along the transect was summed and then divided by the total number (30) of possible observations. The relative presence value ranged between 0 for no occurrence to 1 for occurrence along the whole transect. This information provided a general habitat description of the area.

P. sinuosa and epiphyte biomass estimates

Seagrass dry weight biomass was estimated at each site by stratified sampling (Walker 1988). Six $20 \times 20 \text{ cm}$ quadrats were placed haphazardly within a 5 m radius, in the middle of the dominant seagrass bed, at each site. All the above-ground material originating from inside the quadrat was collected and frozen. On return to the laboratory, each sample was scraped with an industrial razor blade to remove the erect algal epiphytes (encrusting epiphytes were not removed) and separated into red (Rhodophyta), green (Chlorophyta) and brown (Phaeophyta) algae. Seagrass and epiphytic material were dried for 24 hours and then weighed to give an estimate of dry weight in grams (Neverauskas 1987). These values were extrapolated to dry weight (dw) biomass of seagrass and epiphytes in grams per unit area (g m^{-2}). The epiphyte to leaf (E/L) ratio was calculated for each site and sampling period. This is the ratio of epiphyte dry weight biomass to seagrass dry weight biomass (Neverauskas 1987).

As extensive amounts of seagrass wrack accumulated over winter; in July the cover of seagrass wrack on the beach was quantified along a 1.5 km stretch of shoreline westward from the entrance of the Vasse-Wonnerup Estuary. Large accumulations of seagrass wrack (mainly *Posidonia sinuosa*) were present on the sandy beach out to 100 m from shore, between Vasse-Wonnerup Estuary and Vasse Diversion drain in July. The cover was estimated at 30 m intervals along a ten metre wide strip from the shore-line up the beach. Along a 350 m stretch, the volume of wrack was determined by measuring the

height, width and depth of each wrack "lump". The area from which this total volume of seagrass may have originated was calculated by estimating dry weight biomass of the wrack from the volume of wrack present (Hansen & Brearley, *pers comm*) and then relating this to average biomass (g m^{-2}) in the area offshore.

Results

Physical conditions

Drain flow and water colour. During summer (December to February) and in April, the water in Geographe Bay was calm and clear; the bottom was visible at 5 m depth. None of the drains or the estuary were flowing. In July, all drains and the estuary were flowing rapidly, discharging a large volume of brown-coloured fresh water. Vasse Diversion Drain was flowing fastest followed by the Vasse-Wonnerup Estuary and then Buayanup drain. The water offshore was extremely turbid, the bottom was not visible in 1 m of water, and brown discolouration was visible 3 km out to sea. This discolouration extended from Toby's drain to Forrest Beach. There was no

discolouration in the water column at Dunsborough, the reference site. In September, the estuary had ceased to flow but the two drains were flowing more slowly, with Buayanup drain flowing faster than Busselton drain.

Temperature. Water temperature peaked at the end of summer (February) with a mean of 21.6 ± 0.4 °C. The mean minimum temperature was recorded in July at 14.8 ± 0.4 °C (Table 1). There was a gradient of temperatures along the coast in summer with 1 °C cooler temperatures in the south-west of the bay in comparison to the north-easterly sites.

Light. The amount of light above the seagrass canopy, at 5 m depth, also peaked in summer (mean of $620 \mu\text{mol m}^{-2} \text{s}^{-1}$) and was lowest in winter (Table 1). Turbidity increased dramatically in winter at sites associated with drains. The attenuation coefficient was higher in July and September than in January and April (0.22 - 0.96). There was a slight increase in attenuation coefficient (0.13 - 0.35) in winter at the site not associated with a drain (Table 1).

Water column phytoplankton concentration. The water column chlorophyll *a* concentration was generally low over the year (Table 2). The highest chlorophyll *a*

Table 1

Temperature, light and attenuation coefficients in Geographe Bay. Temperature is averaged over four sites. Both temperature and irradiance were measured at the bottom of the water column, above the seagrass canopy. Site 1 is Dunsborough, the site without an associated drain. Sites 3, 4 and 5 are all associated with drains, and are Buayanup drain, Vasse-Diversion drain and Vasse-Wonnerup Estuary respectively. Values are mean ($\pm$ standard deviation, with a sample size of 4, except July with a sample size of 2).

	Temperature (°C)	Irradiance ($\mu\text{mol m}^{-2} \text{s}^{-1}$)					Light attenuation				
		1	3	4	5	Mean	1	3	4	5	Mean
Jan. 1994	20.8 ± 0.4	830	400	565	700	624 ± 106	0.113	0.101	0.081	0.217	0.128 ± 0.04
Apr 1994	21.3 ± 0.2	234	269	197	292	248 ± 24	0.134	0.125	0.054	0.117	0.108 ± 0.02
July 1994	14.8	ns	ns	ns	ns		0.350	ns	ns	0.960	0.655
Sep 1994	15.5 ± 0.1	50	43	41	4	35 ± 12	0.215	0.340	0.28	0.385	0.305 ± 0.04
Jan 1995	21.6 ± 0.3	550	570	430	420	493 ± 45	0.062	0.008	0.105	0.167	0.086 ± 0.04

Table 2

Temporal and spatial variation in *P. sinuosa* biomass, epiphyte biomass and chlorophyll *a* concentration at Geographe Bay in 1994-1995. Values are mean ($\pm$ standard error, with a sample size of 6).

Month	<i>P. sinuosa</i> biomass (g m^{-2})				Algal epiphyte biomass (g m^{-2})				Chlorophyll <i>a</i> ($\mu\text{g l}^{-1}$)			
	Sites 1	3	4	5	1	3	4	5	1	3	4	5
Jan 1994	234 ± 32	469 ± 40	287 ± 47	234 ± 32	5 ± 2	1 ± 1	8 ± 3	26 ± 9	0.12	0.22	0.22	0.20
April 1994	113 ± 19	282 ± 31	180 ± 38	162 ± 27	10 ± 3	12 ± 2	9 ± 2	2 ± 1	0.08	0.14	0.18	0.12
July 1994	152 ± 20	ns	ns	116 ± 15	24 ± 6	ns	ns	0 ± 0	ns	ns	ns	0.63
Sept 1994	154 ± 26	196 ± 17	152 ± 20	119 ± 24	17 ± 5	3 ± 1	1 ± 1	0 ± 0	0.12	0.17	0.23	0.49
Jan 1995	159 ± 21	281 ± 28	244 ± 29	271 ± 11	2 ± 1	5 ± 2	11 ± 3	3 ± 1	0.09	0.27	0.13	0.13

Table 3

Species recorded at eight study sites in Geographe Bay, 1993 and 1994.

Site	1	2	3	4	5	6	7	8
Seagrass								
<i>Posidonia sinuosa</i>	+	+	+	+	+	+	+	+
<i>Posidonia angustifolia</i>		+				+		+
<i>Amphibolis antarctica</i>	+	+	+	+	+	+	+	+
<i>Amphibolis griffithii</i>	+	+			+	+	+	
<i>Halophila ovalis</i>	+				+	+	+	+
Macroalgae								
Chlorophyta								
<i>Caulerpa cactoides</i>							+	
<i>Caulerpa</i> sp					+	+	+	+
<i>Codium</i> sp								+
<i>Halimeda cuneata</i>							+	+
<i>Rhipiliopsis</i> sp								+
<i>Caulocystis uvifera</i>						+		
<i>Dictyopteris muelleri</i>						+	+	
<i>Ecklonia radiata</i>						+	+	
<i>Hydroclathrus clathratus</i>								+
<i>Lobophora variegata</i>	+							
<i>Padina</i> sp	+					+	+	
<i>Scaberia aghardii</i>	+				+	+	+	
<i>Sargassum</i> sp					+	+	+	+
Rhodophyta								
<i>Asparagopsis armata</i>						+		+
<i>Dictymenia sonderi</i>								+
<i>Gelidium asperum</i>								+
<i>Gelidium</i> sp							+	
<i>Gigartina disticha</i>								+
<i>Laurencia clavata</i>								+
<i>Osmundaria prolifera</i>						+		+
<i>Phacelocarpus alatus</i>								+
Epiphytic algae								
<i>Cladophora montagneana</i>			+	+	+	+	+	+
<i>Cladophora dalmatica</i>	+		+	+	+	+	+	+
<i>Polycerea nigrescens</i>	+	+			+	+		+
<i>Pachydictyon paniculatum</i>	+	+	+	+	+	+	+	
<i>Pachydictyon polycladum</i>	+	+	+	+	+	+	+	
<i>Metagoniolithon chara</i>	+	+		+	+	+		+
<i>Lenormandia marginata</i>					+	+		
<i>Chondria</i> sp								+
Microalgae								
<i>Mastogloia</i> sp	+	+	+	+	+	+		
<i>Chroococcus</i> sp	+	+	+	+	+	+	+	+

concentration was recorded in winter at Vasse-Wonnerup Estuary ($0.63 \mu\text{g l}^{-1}$) and the lowest in summer at Dunsborough ($0.08 \mu\text{g l}^{-1}$). The average concentration over the year at the four sites was $0.22 \pm 0.05 \mu\text{g l}^{-1}$.

Benthic communities - general description. Seagrass and algal species found in Geographe Bay are detailed in Table 3. The benthic substrata of Geographe Bay can be divided into three main categories; sandy substrata, a combination of sandy substrata and low relief reef and a combination of low and high relief reef. Sandy substrata

were present in the south-western portion of the bay between Dunsborough and Vasse-Wonnerup Estuary. These areas were dominated by monospecific meadows of *Posidonia sinuosa*, with *Amphibolis antarctica* and *Amphibolis griffithii* (J Black) den Hartog often on the periphery of the meadows. Closer to Dunsborough the cover of *Amphibolis* spp increased and a number of large meadows occurred. The brown macroalga, *Scaberia aghardii* Greville, was also present in patches.

Sites with sandy substratum and low relief reef were found north of Wonnerup, around Forrest Beach, with a combination of seagrasses (*P. sinuosa*, *A. antarctica*, *A. griffithii* and *Halophila ovalis* (R Brown) JD Hooker) in small patches. Dominant macroalgae included *Osmundaria prolifera* Lamouroux, *Scaberia aghardii*, *Sargassum* spp, *Caulerpa* spp and *Padina* spp. Plate corals and sponges were also present.

At Capel and 5 Mile Brook Diversion, there was low and high relief reef. There were small patches of the seagrasses, *A. griffithii* and *A. antarctica*, at Capel. *Posidonia angustifolia* was found on sandy bottoms surrounding high relief reef, further north. Most common benthic macroalgae were the kelp, *Ecklonia radiata* (C Agardh) J Agardh, and *Sargassum* spp. Many small red turf algae were present along with erect red and green algae such as *Caulerpa* spp.

Three main types of epiphytes were noted in the bay; macroalgal epiphytes (Table 3), diatom aggregations and cyanobacterial aggregations. There was temporal variation in these epiphytes, with *Cladophora* Kuetzing (Chlorophyta), *Pachydictyon* and *Polycerea* (Phaeophyta), dominant in summer and red algae such as *Metagoniolithon* Ducker more common in winter. *Amphibolis* bore a greater load of red algal epiphytes than did *Posidonia*. An extensive bloom of *Cladophora* occurred in December of 1993 and 1994 at Capel River and Forrest Beach. This disappeared after one month.

Mastogloia Hustedt (Bacillariophyta) aggregations were found in the south-western portion of the bay. They increased in cover over summer. After a storm in summer, the majority of the aggregations were gone and remained absent throughout the rest of the year. *Chroococcus* Nageli (cyanobacteria) aggregations were present at all sites. They increased in cover over summer, especially at Vasse River Diversion drain and Vasse-Wonnerup Estuary, but were not present during the rest of the year.

***P. sinuosa* biomass.** Highest biomass was recorded in summer and lowest in winter (Table 2). The mean maximum biomass for *P. sinuosa* occurred during summer (470 g m⁻² at Buayanup drain) and the mean minimum biomass occurred in winter (115 g m⁻² at Vasse-Wonnerup Estuary). Buayanup drain had the highest biomass of the four sites examined.

Epiphytic algal biomass. There were temporal and spatial variations in the epiphytic communities on the seagrass (Table 2) with two main patterns in algal epiphyte biomass. At the site without a drain, the highest epiphyte biomass was recorded in winter (24 g m⁻²) and the lowest in summer (2 g m⁻²). However at sites with drains, the highest biomass in summer (26 g m⁻²), and the lowest in winter (0.1 g m⁻²). The E/L ratio never exceeded 0.2 throughout the year.

Seagrass wrack accumulations. Cover of beached seagrass wrack ranged between 0 to 45% of the area surveyed at each ten meter interval. Along a 1.5 km stretch of beach the average cover was 24%. Along a 350 m stretch of beach, the total volume of wrack present was estimated at 81 000 m³.

Discussion

The marine benthic communities examined at 5 m depth in Geographe Bay were dominated by seagrass, particularly *Posidonia*, although sites with more reef had more *Amphibolis*. The seasonal variation in seagrass biomass was relatively consistent and within the range of other studies (Hillman *et al.* 1989). Algal communities were typical of Western Australian coastal reefs and seagrass beds. There were no large accumulations of drift algae, in summer or winter. Algal epiphytes species and the change of species seasonally were typical of seagrass communities along the south-western Australian coast (Hillman & Morrison 1994).

Extensive wrack deposits were observed in winter, mainly composed of seagrass as reported elsewhere on the Western Australian coastline (Kirkman & Walker 1989). The volume of wrack accumulated on a 350 m stretch of beach had an estimated dry weight biomass of 2-8.0 10⁶ kg dw. This equates to 4.8 km² of seagrass at maximum biomass. The area that this is likely to originate from is 15 km² of seagrass meadow.

A number of parameters measured in Geographe Bay varied over the year. The water column temperature decreased from a summer and autumn maximum of 21.6 °C to a winter and spring minimum of 14.8 °C. The 6.8 °C reduction in temperature between summer and winter is expected for this latitudinal position (Dring 1992). The water temperature in Geographe Bay was 1 °C less than that recorded for Perth coastal waters at the same depth (Buckee *et al.* 1994). This probably reflects the cold Capes Current which moves northward along Geographe Bay and the warmer Leeuwin Current which passes Perth (Cresswell & Golding 1980).

Vertical light attenuation coefficient increased in July and September, indicating that light was dissipated more quickly through the water column. Phytoplankton and organic and inorganic particles held within the water column all affect attenuation (Kirk 1994). High turbidity from suspended particles and tannins discharged from the drains increased the attenuation in July and September, at sites with drains. The accumulation and breakdown of seagrass in nearshore waters in July, especially at Vasse-Wonnerup Estuary also contributed to increased light attenuation.

Light and temperature often determine the relative growth rates of algae, with lower temperatures and irradiances interacting to reduce relative growth rates (Round 1981). In July and September, at the drain sites, very few epiphytes were found on *P. sinuosa*. The low irradiance at the seagrass bed may have restricted epiphyte growth. Dunsborough, the site without the drain, had the highest epiphyte load in July and attenuation was not as high as the other drain sites. Algal epiphytes were most likely not limited by light at this site. Dunsborough was the only site conforming to the pattern described in the literature of higher epiphyte loads on *P. sinuosa* in winter (Hillman & Morrison 1994).

Phytoplankton concentrations (estimated from chlorophyll *a*) were low through out the year at all sites, with no blooms detected. There was a noticeable increase in phytoplankton in the water column at Vasse-Wonnerup Estuary in July and September. This may be a

reflection of higher nutrient concentrations in the water column at this time and follows the expected seasonal pattern of spring blooms.

The biomass of *P. sinuosa* seagrass varied seasonally and was similar to values described in the literature (Hillman *et al.* 1989). There was a three fold reduction in seagrass biomass from 350 g m⁻² in summer to 120 g m⁻² in winter. This seasonal variation is influenced by leaf loss through storm events and shedding of leaves after growth in summer (Patriquin 1975).

Studies of net production in the seagrass *P. sinuosa* under different light and temperature regimes have estimated the minimum temperature and light required for positive net growth (Masini *et al.* 1995). In relation to these studies, net production of seagrass in Geographe Bay at Dunsborough, Buayanup and Vasse-Diversion drain, would be positive from September to April, over spring, summer and autumn, with temperatures greater than 15 °C and irradiance at the top of the seagrass canopy greater than 30 µmol m⁻² s⁻¹. At Vasse-Wonnerup Estuary in September, irradiance at the top of the seagrass canopy was 4 µmol m⁻² s⁻¹ and in July this would be less because attenuation coefficients were much higher at this time. Therefore at Vasse-Wonnerup Estuary between July and September, net production is likely to be negative. Respiration would be greater than photosynthesis and a net loss of organic carbon could be expected. A mechanism for maintaining growth over winter would be required for seagrasses with net negative productivity. Pirc (1989) found that *P. oceanica* (L) Delile was able to store carbon and nitrogen in the rhizomes during summer and autumn, which could be mobilised and accessed for leaf growth in winter. A similar mechanism could maintain *P. sinuosa* in winter when light and temperature limit photosynthesis. The seagrass at Dunsborough, where light did not fall below 50 µmol m⁻² s⁻¹, could maintain a positive net production throughout the year.

A reduction in light reaching a seagrass bed for extended periods, by epiphyte shading or high turbidity in the water column, can cause a decrease in density of seagrass (Neverauskas 1987; Cambridge *et al.* 1986). Limited light during winter from high turbidity in the water column at Vasse-Wonnerup Estuary and the shading in summer by cyanobacterial aggregations at Vasse Diversion drain and Vasse-Wonnerup Estuary make these sites susceptible to reduction in seagrass density. However to test this hypothesis a longer period of study would be required.

Potential symptoms of eutrophication noted in this study were blooms of *Cladophora* at Capel and Forrest Beach in early summer (December 1993 and 1994). These blooms are expected seasonal phenomena, where elevated nutrient concentrations from winter and warmer conditions promote algal growth. If such a bloom was to continue for extended periods, detrimental effects such as reduced oxygen concentrations and shading effects could occur.

There were also aggregations of diatoms and cyanobacteria. Cyanobacteria are often present in eutrophic systems (Hallegraeff 1992). In Geographe Bay, the increase in relative presence of cyanobacteria and diatom aggregations over the summer may be attributed to warmer temperatures and calm conditions. Some

cyanobacteria can fix nitrogen and therefore can proliferate in nitrogen-poor conditions if required phosphorus is available (Smith 1984). Cyanobacterial aggregations were dominant around Busselton and diatom aggregations were dominant in the southern end of the study area, near Dunsborough. When strong wind and wave action were present, the blooms were dispersed. There were no blooms in winter and after summer storms; all diatom aggregations disappeared. Aggregations of diatomaceous mucopolysaccharides ("slime") have also been observed in the mediterranean sea, in summer, under low nutrient concentrations in the water column, less than 1 µg l⁻¹ nitrate (Stirn 1994; I M Munda, pers. comm.). The nitrate concentration varied from 1 to 3 µg l⁻¹ in the waters of Geographe Bay in summer (unpublished observation).

Conclusions

This study has identified seasonal variation in physical and biological conditions in the nearshore waters of Geographe Bay. They conform to the expected seasonal patterns in a mediterranean shallow seagrass system. The seagrasses at most sites are in a healthy condition, without exceptional epiphytic loads. Blue-green and diatom aggregations were the only symptom of eutrophication noted in this study and require further study.

Acknowledgments: This study was funded by the Water Authority of Western Australia, South-West Division. Additional funding was provided by a UWA Jennifer Arnold Memorial Scholarship to K McMahon. D Lord contributed to this research and provided comments on the manuscript. We are grateful to G Moore, E Cole, C Sim, T Carruthers, J Verduin, A Markey, M Coyne, A Maskew, M Gunstan, M Delval, M Jury and N Marba for valuable assistance with field work.

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Foraminifera from Exmouth Gulf, Western Australia

D W Haig

Department of Geology & Geophysics, University of Western Australia, Nedlands WA 6907
email: dhaig@geol.uwa.edu.au

Manuscript received January 1997; accepted September 1997.

Abstract

Two hundred and thirty-six benthonic species and six planktonic species are identified among Foraminifera present in Holocene sediment of Exmouth Gulf, in a water depth of 5-30 m. The benthonic microfauna comprises 20 agglutinated species (including 9 Lituolida, 1 Trochamminida, and 10 Textulariida), 74 porcellaneous species (Miliolida), and 142 hyaline species (including 4 Spirillinida, 27 Lagenida, 37 Buliminida, and 75 Rotaliida). Abundant species, at least at one site, include *Ammotium australiensis*, *Textularia foliacea*, *Textularia lateralis*, and *Textularia oceanica* among the agglutinated types; *Parahauerinoides fragilissimus*, *Peneroplis pertusus*, *Planispirinella exigua*, *Pseudomassilina australis*, *Quinqueloculina arenata*, *Q. philippinensis*, *Q. sp 8*, *Sigmoihauerina involuta*, *Sorites marginalis*, *Triloculina tricarinata* among the porcellaneous species; and *Ammonia parkinsoniana*, *Amphistegina lessonii*, *A. sp cf A. papillosa*, *A. radiata*, *Asterorotalia gaimardi*, *Cibicides sp cf C. refulgens*, *Discorbinoides patelliformis*, *Elphidium sp cf E. advenum*, *E. crispum*, *E. sp 1*, *Heterostegina depressa*, *Operculina ammonoides*, *Pararotalia nipponica*, and *Rosalina cosymbosella* among the hyaline (Rotaliida) species.

Introduction

There are no comprehensive published records of foraminiferal faunas from inner neritic environments along the 2500 km Western Australian coast between Derby and Augusta (Fig 1), and this region remains one of the least documented for Foraminifera on any continent (see review by Murray 1991). The few records that exist detail only part of the fauna and illustrate only a few species. Betjeman (1969) presented a broad description of the distribution of Foraminifera on the western continental shelf, based on scattered samples (one in the western Exmouth Gulf) from latitudes 18 °S to 34 °S. Mention was made of 191 species and 38 of these were illustrated. From the data presented in Betjeman's (1969) paper and the material from his study housed in the Museum collection of the Department of Geology and Geophysics at the University of Western Australia, it is not possible to confirm the identifications of many of the species named but not illustrated in the article.

The most comprehensive reports of modern Foraminifera in Western Australia are studies by Mackenzie (1962) and Quilty (1977) on south coast estuarine and embayment faunas, and a major taxonomic study by Loeblich & Tappan (1994) who described and illustrated 946 species from sediment samples collected from the Sahul Shelf and Timor Trough (within a water depth range of 19 - 2716 m). The Sahul Shelf monograph of Loeblich & Tappan (1994) illustrates species by scanning electron micrographs which allow detailed comparison with Foraminifera found elsewhere along the shelf. The documentation of species along the coast, using a consistent nomenclature, will enhance the utility of the Foraminifera, particularly in biogeographic differentiation within this region.

The purpose of this paper is to provide a comprehensive record of the foraminiferal species present in Holocene sediment in Exmouth Gulf, a major embayment on the central north-west coast of Western Australia (Figs 1, 2). This taxonomic record is a prerequisite to studies that may elucidate aspects of sedimentology, ecology, and biogeography.

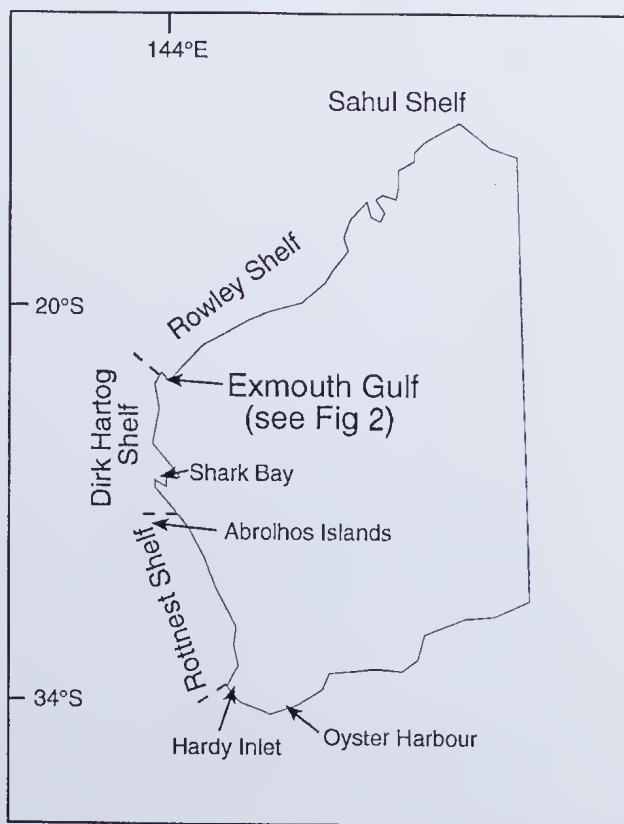


Figure 1. Map of Western Australia showing location of Exmouth Gulf and main sectors of the western continental shelf.

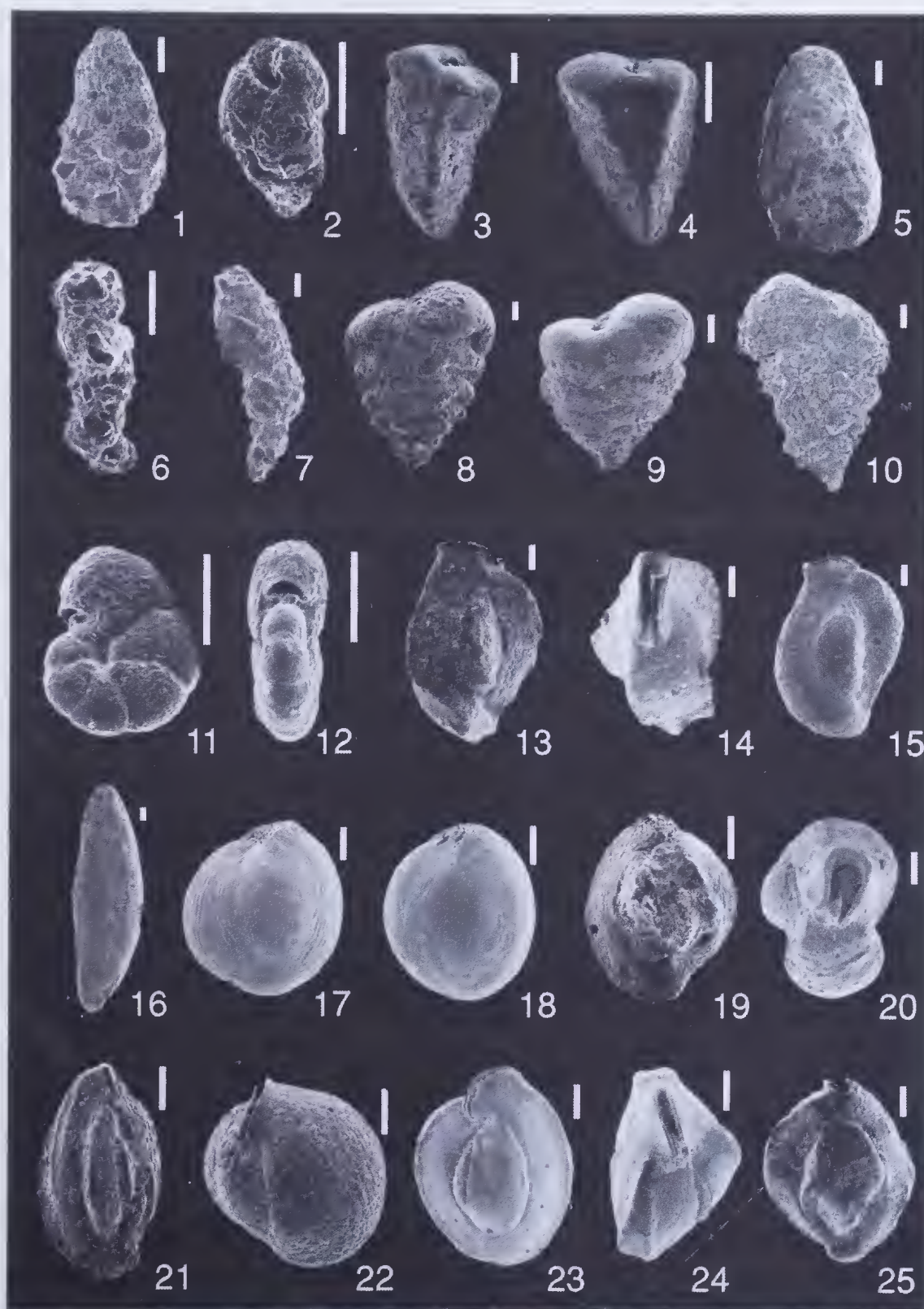


Figure 3. Agglutinated (1-12) and porcellaneous (13-25) Foraminifera (bar scales = 0.1 mm). 1, *Ammotium australiensis* (Collins) from sample 1134. 2, *Eggerelloides australis* (Collins) from sample 1116. 3, *Gaudryina convexa* (Karrer) from sample 1027. 4, *Gaudryina* sp from sample 1021. 5, *Nouria polymorphinoides* Heron-Allen & Earland from sample 999. 6, ?*Reophax* sp 1 from sample 1114. 7, *Reophax* sp 2 from sample 1134. 8, *Textularia kerimbaensis* Said from sample 1029. 9, *Textularia lateralis* Lalicker from sample 1134. 10, *Textularia occidentalis* Heron-Allen & Earland from sample 1134. 11, 12, *Veleroninoides jeffreysii* (Williamson) from sample 1029. 13, 14, *Affinetrina bassensis* (Parr) from sample 1095. 15, 20, *Affinetrina* sp from sample 1080. 16, *Borelis schlumbergeri* (Reichel) from sample 999. 17, 18, *Cribromiliolinella milletti* (Cushman) from sample 999. 19, *Hauerina* sp from sample 1024. 21, *Miliolinella* sp cf *M. baragwanathi* (Parr) from sample 1008. 22, *Miliolinella* sp from sample 1024. 23, 24, *Quinqueloculina barnardi* Rasheed from sample 1134. 25, *Quinqueloculina distortaqueata* Cushman from sample 1008.



Figure 4. Porcellaneous (1-24) and hyaline-spirilline (25-27) Foraminifera (bar scales = 0.1 mm). 1, *Quinqueloculina neostriatula* Thalmann from sample 1128. 2, 3, *Quinqueloculina pittensis* Albani from sample 1134. 4, 5, *Quinqueloculina poeyana* d'Orbigny from sample 1024. 6, 7, *Quinqueloculina* sp1 from sample 1027. 8, 9, *Quinqueloculina* sp 3 from sample 1134. 10, 11, *Quinqueloculina* sp 4 from sample 1134. 12, 13, *Quinqueloculina* sp 5 from sample 999. 14, 15, *Quinqueloculina* sp 6 from sample 1134. 16, 17, *Quinqueloculina* sp 7 from sample 1134. 18, 19, *Quinqueloculina* sp 8 from sample 1134 (different specimens). 20, 21, *Sigmoilinella tortuosa* Zheng from sample 999. 22, *Spiroloculina angulata* Cushman from sample 1027. 23, *Triloculina barnardi* Rasheed from sample 1024. 24, *Triloculina papuaensis* Rasheed from sample 1128. 25-27, *Mychostomina* sp from sample 1008 (25 and 26, same specimen).



Figure 5. Hyaline Foraminifera: Spirillinida (1,2), Lagenida (3-10), Buliminida (11-25) and Rotaliida (26, 27) [bar scales = 0.1 mm]. 1, 2, *Conicospirillinoidea* sp from sample 1091. 3, *Dentalina* sp 1 from sample 1024. 4, *Dentalina* sp 2 from sample 1010. 5, *Fissurina* sp 1 from sample 1134. 6, *Fissurina* sp 2 from sample 1029. 7, *Glandulina* sp from sample 1008. 8, *Guttulina* sp from sample 999. 9, *Pseudoglandulina* sp from sample 999. 10, *Webbinella* sp from sample 1029 (cemented to shell fragment). 11, *Angulogerina* sp 1 from sample 1067. 12, *Angulogerina* sp 2 from sample 999. 13, *Bolivina striatula* (Cushman) from sample 999. 14, *Bolivina* sp 1 from sample 999. 15, *Bolivina* sp 2 from sample 999. 16-18, *Elongobula milleti* (Cushman) from sample 1134 (different specimens). 19, *Evolvocassidulina* sp from sample 1021. 20, *Globocassidulina* sp from sample 1095. 21, *Reussella* sp 1 from sample 999. 22, *Reussella* sp 2 from sample 1134. 23-25, *Reussella* sp 3 from sample 1134 (different specimens). 26, *Acervulina mahabeti* (Said) from sample 1021. 27, *Ammonia* sp from sample 1023.

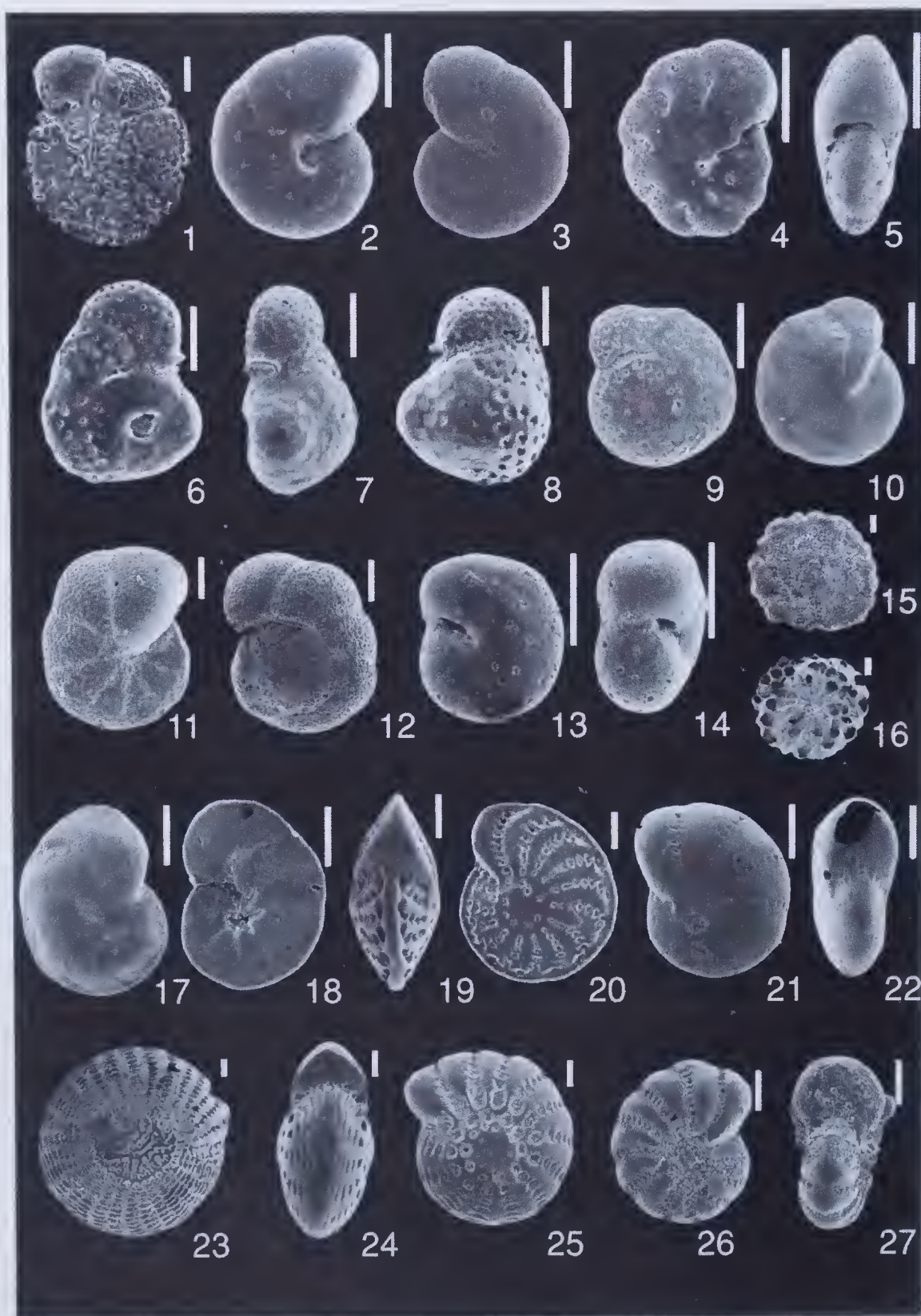


Figure 6. Hyaline Foraminifera: Rotaliida (bar scales = 0.1 mm). 1, *Ammonia* sp from sample 1023 (same specimen as Fig 4:27). 2, 3, *Anomalinulla glabrata* (Cushman) from sample 999. 4, 5, *Astrononion* sp from sample 1008. 6-8, ?*Cibicides* sp from sample 999. 9, 10, *Cibicoides basilanensis* (McCulloch) from sample 1134. 11, 12, *Cibicoides* sp from sample 1027. 13, 14, *Cribraggina socorroensis* McCulloch from sample 999. 15, 16, *Cymbaloporella tabellaeformis* (Brady) from sample 1029 (chambers, shown in 16 on ventral side of test, are broken). 17, 18, *Discorbinella rhodiensis* (Terquem) from sample 1134 (different specimens). 19, 20, *Elphidium* sp cf *advenum* (Cushman) from sample 1134. 21, 22, *Elphidium albanii* Hayward from sample 1134. 23, *Elphidium* sp cf *E. craticulatum* (Fichyel & Moll) from sample 1135. 24, 25, *Elphidium mortonbayensis* Albani & Yassini from sample 1134. 26, 27, *Elphidium oceanicum* Cushman from sample 1134 (different specimens).

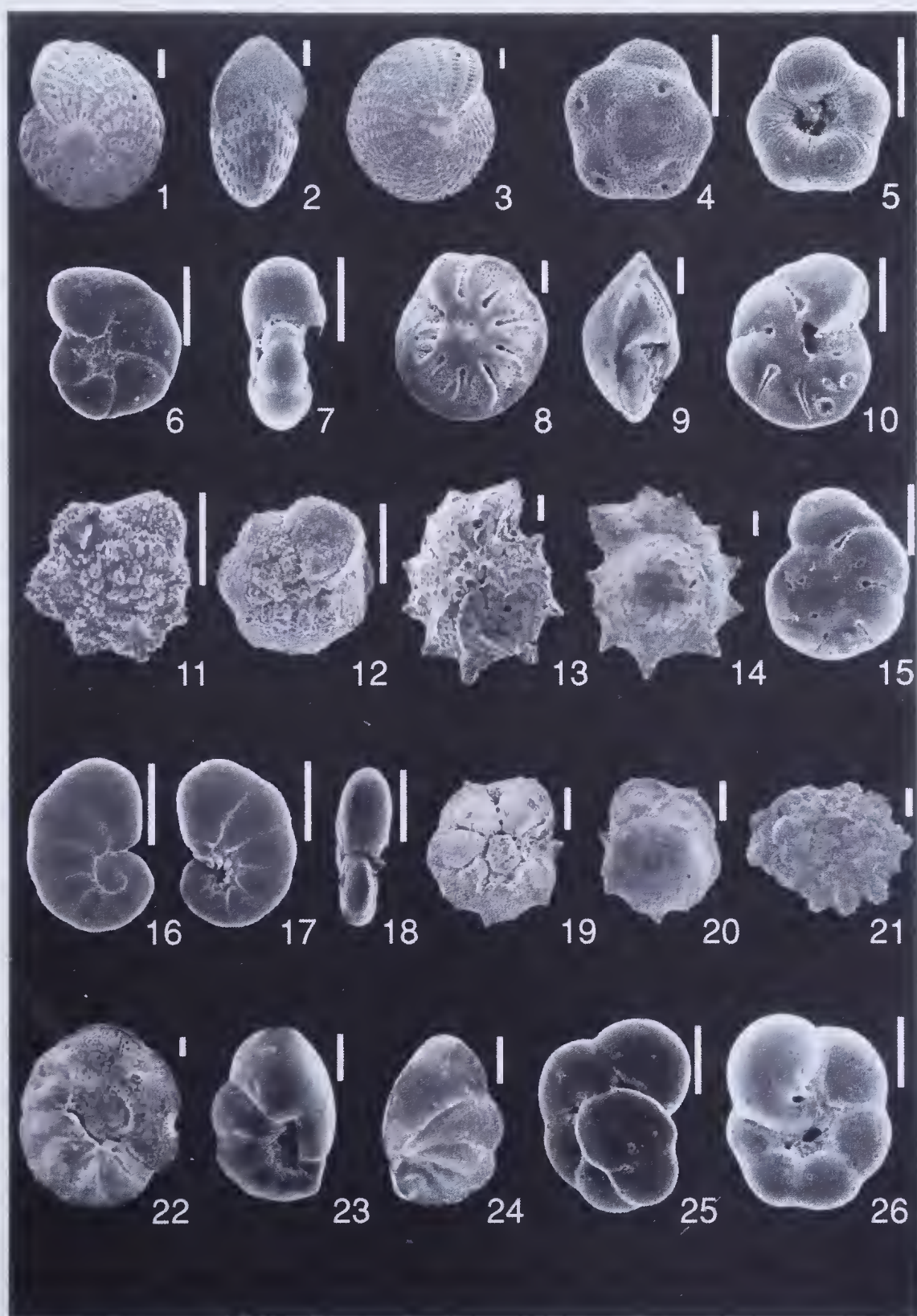


Figure 7. Hyaline Foraminifera: Rotaliida (bar scales = 0.1 mm). 1, 2, *Elphidium* sp cf *E. striatopunctatus* (Fichtel & Moll) from sample 1134 (different specimens). 3, *Elphidium* sp, from sample 1134. 4, 5, *Glauvoluta* sp from sample 999. 6, 7, ?*Haynesina* sp from sample 1067. 8, 9, *Lamellodiscorbis melbyae* Hansen & Revets from sample 999. 10, 15, *Monspeliensis* sp 2 from sample 1135. 11, 12, *Murrynella murrayi* (Heron-Allen & Earland) from sample 999 (different specimens). 13, 14, *Neorotalia calcar* (d'Orbigny) from sample 999. 16-18, *Nonionoides* sp from sample 1095. 19, 20, *Pararotalia nipponica* (Asano) from sample 1134. 21, *Planogypsina acervalis* (Brady) from sample 999. 22, *Poreponides lateralis* (Terquem) from sample 1116. 23, 24, ?*Saintclairoides* sp from sample 999. 25, 26, *Schwartzia* sp from sample 1067.

Order Textulariida

Clavulina multicamerata Chapman.

Clavulina serventyi Chapman & Parr; Mackenzie 1962, Pl 1, Fig 14, Oyster Harbour.

Clavulina multicamerata Chapman; Loeblich & Tappan 1994, Pl 47, Figs 11-15, Sahul Shelf.

Clavulina pacifica Cushman.

Clavulina pacifica Cushman; Mackenzie 1962, Pl 1, Fig 13, Oyster Harbour; Loeblich & Tappan 1994, Pl 47, Figs 16-24, Sahul Shelf.

Sahulia barkeri (Hofker); [Textularia].

Sahulia barkeri (Hofker); Loeblich & Tappan 1994, Pl 32, Figs 1-8, Sahul Shelf.

Textularia cushmani Said.

Textularia cushmani Said; Loeblich & Tappan 1994, Pl 35, Figs 1-4, Sahul Shelf.

Textularia foliacea Heron-Allen & Earland.

Textularia foliacea Heron-Allen & Earland; Loeblich & Tappan 1994, Pl 34, Figs 6-14, Sahul Shelf.

Betjeman (1969) recorded *T. foliacea* as a widespread species on the Western Australia shelf.

Textularia kerimbaensis Said; Figure 3:8.

Textularia lateralis Lalicker; Figure 3:9.

Textularia oceanica Cushman.

Textularia oceanica Cushman; Loeblich & Tappan 1994, Pl 40, Figs 15-17, Sahul Shelf.

Textularia occidentalis Heron-Allen & Earland; Figure 3:10.

This may be an extreme variant of *T. foliacea*, differing from typical *T. foliacea* by a much more flaring test.

Textularia sp.

Textularia secasensis; Loeblich & Tappan 1994, Pl 39, Figs 8-14 (not *T. secasensis* Lalicker & McCulloch), Sahul Shelf.

T. secasensis has a subacute peripheral margin in the adult stage that differs from the broadly rounded margin of the present species.

Order Miliolida

Affinetrina bassensis (Parr); [Triloculina]; Figure 3:13,14.

This species was recorded by Betjeman (1969) as *Triloculina bassensis*, abundant in the Abrolhos Islands and at stations north of the islands.

Affinetrina sp; Figure 3:15,20.

This species is related to some of the forms included originally in *Miliolina kerimbatica* Heron-Allen & Earland 1915 (e.g. Pl 43, Fig 19 of Heron-Allen & Earland, 1915).

Amphisorus hemprichii Ehrenberg.

Marginopora vertebralis Quoy & Gaimard; Mackenzie 1962, Pl 3, Fig 15, Oyster Harbour.

? *Marginopora vertebralis* Blainville; Quilty 1977, Fig 25 (juvenile specimen), Hardy Inlet.

Amphisorus hemprichii Ehrenberg; Loeblich & Tappan 1994, Pl 109, Figs 7-13; Pl 110, Figs 6,7, Sahul Shelf.

Marginopora vertebralis is distinguished from *Amphisorus hemprichii* by having multiple layers of chamberlets rather than two-layers in the adult stage. Betjeman's (1969) determination of *M. vertebralis* apparently refers to *A. hemprichii*, based on specimens which he mounted on slides in the UWA collection.

Articulina alticostata Cushman.

Articulina alticostata Cushman; Loeblich & Tappan 1994, Pl 104, Figs 5-10, Sahul Shelf.

This species was recorded by Betjeman (1969) as being more abundant on northern rather than southern sectors of the Western Australian shelf.

Articulina mucronata (d'Orbigny); [Vertebralina].

Articulina mucronata (d'Orbigny); Loeblich & Tappan 1994, Pl 104, Figs 1-4, Sahul Shelf.

Betjeman (1969) recorded this species as *Articulina pacifica* Cushman and found that it ranged north from Exmouth Gulf to the Rowley Shelf.

Articulina sp.

Articulina carinata Cushman; Loeblich & Tappan 1994, Pl 104, Figs 11-18, Sahul Shelf.

This species lacks the distinctly keeled periphery and numerous fine longitudinal costae that characterise *A. carinata* Cushman.

Borelis schlumbergeri (Reichel); [Neovalveolina]; Figure 3:16.

This may be the species recorded by Betjeman (1969) as *Alveolinella boscii* from Exmouth Gulf and the Rowley Shelf.

Cornuspira planorbis Schultze.

Cornuspira planorbis Schultze; Loeblich & Tappan 1994, Pl 56, Figs 1-7, Sahul Shelf.

Coscinospira acicularis (Batsch); [Nautilus (Lituus)].

Coscinospira acicularis (Batsch); Loeblich & Tappan 1994, pl. 107, Figs 5-10, Sahul Shelf.

Cribromiliolinella milletti (Cushman); [Hauerina]; Figure 3:17,18.

Miliola sp A of Betjeman 1969, Pl 18, Fig 23, Rowley Shelf.

Dendritina ambigua (Fichtel & Moll); [Nautilus].

Dendritina ambigua (Fichtel & Moll); Loeblich & Tappan 1994, Pl 108, Figs 1-4, Sahul Shelf.

Edentostomina cultrata (Brady); [Miliolina].

Edentostomina cultrata (Brady); Loeblich & Tappan 1994, Pl 63, Figs 8-12, Sahul Shelf.

Euthymonacha polita (Chapman); [Peneroplis (Monalysidium)].

Euthymonacha polita (Chapman); Loeblich & Tappan 1994, Pl 109, Figs 1-6, Sahul Shelf.

Hauerina sp; Figure 3:19.

The Exmouth Gulf specimens may be juvenile forms of *H. pacifica* Cushman.

Inaequalina disparilis (Terquem); [*Spiroloculina*].

Inaequalina disparilis (Terquem); Loeblich & Tappan 1994, Pl 64, Figs 11-18, Sahul Shelf.

Mikrobelodontos bradyi (Barker); [*Spiroloculina*].

Spiroloculina sp A of Betjeman 1969, Pl 19, Fig 16, Rowley and Dirk Hartog Shelf areas.

Mikrobelodontos bradyi (Barker); Loeblich & Tappan 1994, Pl 66, Figs 1-8, Sahul Shelf.

Miliolinella sp cf *M. baragwanathi* (Parr); [*Quinqueloculina*]; Figure 3:21.

Quinqueloculina lamarckiana d'Orbigny; Quilty 1977, Fig 18, Hardy Inlet.

The Western Australian specimens lack the distinct obliquely curved costae of the type specimens of *M. baragwanathi*.

Miliolinella philippinensis (McCulloch); [*Pateoris*].

Miliolinella philippinensis (McCulloch); Loeblich & Tappan 1994, Pl 76, Figs 6-11, Sahul Shelf.

Miliolinella pseudooblonga Zheng.

Miliolinella circularis (Bornemann); Mackenzie 1962, Pl 2, Fig 13. Oyster Harbour.

Triloculinella pseudooblonga (Zheng); Loeblich & Tappan 1994, Pl 88, Figs 7-18, Pl 97, Figs 10-12, Pl 98, Figs 1-3, 7-9, Sahul Shelf.

Miliolinella quinquangula Loeblich & Tappan.

Quinqueloculina sp A of Betjeman 1969, Pl 19, Fig 4, Rowley, Dirk Hartog, and Rottneest Shelf areas.

Miliolinella quinquangula Loeblich & Tappan 1994, Pl 82, Figs 14-16, Sahul Shelf.

Miliolinella suborbicularis (d'Orbigny); [*Triloculina*].

Miliolinella sp B of Betjeman 1969, Pl 18, Fig 24, Rottneest Shelf.

Miliolinella suborbicularis (d'Orbigny); Loeblich & Tappan 1994, Pl 89, Figs 1-9, Sahul Shelf.

Miliolinella sp; Figure 3:22.

Nodophthalmidium gracile Collins.

Nodophthalmidium gracile Collins; Loeblich & Tappan 1994, Pl 57, Figs 18,19, Sahul Shelf.

Nubeculina advena Cushman.

Reophax scorpiurus Montfort; Mackenzie 1962, Pl 1, Fig 2, Oyster Harbour.

Nubeculina advena Cushman; Loeblich & Tappan 1994, Pl 59, Figs 1-12, Sahul Shelf.

Parahauerinoides fragilissimus (Brady); [*Spiroloculina*].

Parahauerinoides fragilissimus (Brady); Loeblich & Tappan 1994, Pl 87, Figs 1-6, Sahul Shelf.

As *Hauerina fragilissima*, this species was noted by Betjeman (1969) as having a preference for the tropical-subtropical sectors of the Western Australian shelf.

Peneroplis pertusus (Forskål); [*Nautilus*].

Peneroplis pertusus (Forskål); Mackenzie 1962, Pl 3, Fig 1, Oyster Harbour; Loeblich & Tappan 1994, Pl 110, Figs 1-5, Sahul Shelf.

Peneroplis planatus (Fichtel & Moll); McKenzie 1962, Pl 2, Fig 27, Oyster Harbour.

Betjeman (1969) recorded both *P. pertusus* and *P. planatus* (species considered by the present author to be synonymous) as more abundant on the northern rather than the southern sectors of the Western Australian shelf.

Planispirinella exigua (Brady); [*Hauerina*].

Planispirinella exigua (Brady); Loeblich & Tappan 1994, Pl 57, Figs 7,8, Sahul Shelf.

Betjeman (1969) recorded this species from the Dirk Hartog Shelf and Rowley Shelf.

Pseudomassilina australis (Cushman); [*Massilina*].

Massilina secans var. *tenuistriata* Earland; Mackenzie 1962, Pl 2, Fig 25, Oyster Harbour.

Pseudomassilina australis (Cushman); Loeblich & Tappan 1994, Pl 91, Figs 1-3, Sahul Shelf.

Not *Pseudomassilina australis* (Cushman); Mackenzie, 1962.

Pseudomassilina robusta Lacroix.

Pseudomassilina robusta Lacroix; Loeblich & Tappan 1994, Pl 90, Figs 1-4, Sahul Shelf.

This species is similar to *Pseudomassilina* sp B of Hottinger *et al.* (1993, Pl 45, Figs 1-10).

Pseudopyrgo milletti (Cushman); [*Biloculina*].

Pseudopyrgo milletti (Cushman); Loeblich & Tappan 1994, Pl 89, Figs 10,11, Sahul Shelf.

Pyrgo denticulata (Brady); [*Biloculina*].

Pyrgo denticulata (Brady); Loeblich & Tappan 1994, Pl 92, Figs 1,2, Sahul Shelf.

Pyrgo striolata (Brady); [*Biloculina*].

Pyrgo striolata (Brady); Loeblich & Tappan 1994, Pl 92, Figs 9-15, Sahul Shelf.

Pyrgoella tenuiaperta (Huang); [*Biloculinella*].

Pyrgoella tenuiaperta (Huang); Loeblich & Tappan 1994, Pl 94, Figs 10-14, Pl 99, Figs 10-17, Sahul Shelf.

This species is the same as *Pyrgoella* sp A of Haig (1988, Pl 4, Figs 7,8) and Hottinger *et al.* (1993, Pl 53, Figs 7,8).

Quinqueloculina adiazeta Loeblich & Tappan.

Quinqueloculina adiazeta Loeblich & Tappan 1994, Pl 85, Figs 1-18, Sahul Shelf.

Contrary to Loeblich & Tappan's (1994, p. 48) proposition, this species is not the same as *Q. cf Q. berthelotiana* of Haig (1988, p. 233, Pl 4, Figs 23-26), but resembles *Q. cf Q. rugosa* of Haig (1988, p. 234, Pl 8, Figs 1-5).

Quinqueloculina agglutinans d'Orbigny.

Quinqueloculina agglutinans d'Orbigny; Betjeman 1969, Rowley Shelf and Dirk Hartog Shelf.

Agglutinella agglutinans (d'Orbigny); Loeblich & Tappan 1994, Pl 70, Figs 1-9, Sahul Shelf.

Quinqueloculina arenata Said.

Siphonaperta ammophila (Parr); Mackenzie 1962, Oyster Harbour.

Agglutinella arenata (Said); Loeblich & Tappan 1994, Pl 69, Figs 9-11; Pl 70, Figs 10-15; Pl 74, Figs 10-13, Sahul Shelf.

Quinqueloculina barnardi Rasheed; Figure 3:23,24.

Quinqueloculina crassicarinata Collins.

Quinqueloculina crassicarinata Collins; Loeblich & Tappan 1994, Pl 77, Figs 4-12, Sahul Shelf.

Quinqueloculina distorta Cushman; Figure 3:25.

Quinqueloculina eburnea (d'Orbigny); [*Triloculina*].

Miliolinella oblonga (Montagu); Mackenzie 1962, Oyster Harbour.

Pseudolachlanella slitella Langer; Loeblich & Tappan 1994, Pl 73, Figs 16-18; Pl 101, Figs 1-3, Sahul Shelf.

Quinqueloculina neostriatula Thalmann; Figure 4:1.

Quinqueloculina sp C of Betjeman 1969, Pl 19, Fig 5, Rowley Shelf.

Quinqueloculina parkeri (Brady); [*Miliolina*].

Lachlanella parkeri (Brady); Loeblich & Tappan 1994, Pl 74, Figs 1-6, Sahul Shelf.

Betjeman (1969) recorded this species from the Abrolhos Islands and areas north on the Western Australia shelf.

Quinqueloculina philippinensis Cushman.

Quinqueloculina philippinensis Cushman; Loeblich & Tappan 1994, Pl 81, Figs 1-10, Sahul Shelf.

A broad range of ornament and apertural neck development is included here (similar to the range shown by the Papuan specimens illustrated by Haig 1988). Betjeman (1969) recorded the species from the Dirk Hartog Shelf and Rowley Shelf.

Quinqueloculina pittensis Albani; Figure 4:2,3.

Quinqueloculina subarenaria Cushman; Mackenzie 1962, Pl 2, Fig 22, Oyster Harbour.

Quinqueloculina poeyana d'Orbigny; Figure 4:4,5.

Quinqueloculina poeyana d'Orbigny; Mackenzie 1962, Oyster Bay.

The Papuan specimens identified as *Q. poeyana* by Haig (1988, Pl 7, Figs 15-17) do not belong to this species (see Loeblich & Tappan 1994, p. 51).

Quinqueloculina quinquecarinata Collins.

Quinqueloculina quinquecarinata Collins; Loeblich & Tappan 1994, Pl 79, Figs 13-18, Sahul Shelf.

Quinqueloculina sulcata d'Orbigny.

Quinqueloculina sulcata d'Orbigny; Loeblich & Tappan 1994, Pl 82, Figs 1-6, Sahul Shelf.

Not *Quinqueloculina sulcata* d'Orbigny; Mackenzie 1962.

Quinqueloculina tropicalis Cushman.

Quinqueloculina tropicalis Cushman; Loeblich & Tappan 1994, Pl 78, Figs 13-15, Sahul Shelf.

Quinqueloculina vandiemeniensis Loeblich & Tappan.

Quinqueloculina vandiemeniensis Loeblich & Tappan; Loeblich & Tappan 1994, Pl 83, Figs 1-3, Sahul Shelf.

Quinqueloculina sp 1; Figure 4:6,7.

? *Quinqueloculina granulocostata* Germeraad; Mackenzie 1962, Pl 2, Fig 18, Oyster Harbour.

The costate ornament resembles that in *Q. granulocostata*, but the elongate apertural tooth differs from the bifid tooth in *Q. granulocostata*.

Quinqueloculina sp 2.

Quinqueloculina costata d'Orbigny; Mackenzie 1962, Pl 2, Fig 17, Oyster Harbour.

Quinqueloculina undulata d'Orbigny; Loeblich & Tappan 1994, Pl 81, Figs 11-13, Sahul Shelf.

In Papuan Lagoon assemblages, this species was misidentified as *Q. poeyana* by Haig (1988, p. 234, Pl 7, Figs 15-17).

Quinqueloculina sp 3; Figure 4:8,9.

This species may be the species identified by Loeblich & Tappan (1994, p. 49, Pl 80, Figs 13-15) as *Q. incisa* Vella. It may be related to *Quinqueloculina patagonica* d'Orbigny.

Quinqueloculina sp 4; Figure 4:10,11.

This species is close to the type recorded from the Papuan Lagoon as *Quinqueloculina* sp A by Haig (1988, Pl 9, Figs 1-3).

Quinqueloculina sp 5; Figure 4:12,13.

This species was recorded from the Papuan Lagoon as *Quinqueloculina* sp C by Haig (1988, Pl 9, Figs 7-10).

Quinqueloculina sp 6; Figure 4:14,15.

This species was recorded from the Papuan Lagoon as *Quinqueloculina* cf *Q. oblonga* (Montagu) by Haig (1988, Pl 6, Figs 26-29).

Quinqueloculina sp 7; Figure 4:16,17.

This species may be related to *Quinqueloculina multimarginata* Said.

Quinqueloculina sp 8; Figure 4:18,19.

Quinqueloculina bosciana d'Orbigny; Mackenzie 1962, Pl 2, Fig 16, Oyster Harbour.

In chamber arrangement and apertural detail, this species resembles *Pitella haigi* Langer; but lacks distinct pseudopores.

Rupertianella rupertiana (Brady); [*Miliolina*].

Rupertianella rupertiana (Brady); Loeblich & Tappan 1994, Pl 106, Figs 1-14, Sahul Shelf.

Schlumbergerina alveoliniformis (Brady); [*Miliolina*].

Schlumbergerina alveoliniformis (Brady); Loeblich & Tappan 1994, Pl 72, Figs 9-11, Sahul Shelf.

Sigmamiliolinella australis (Parr); [*Quinqueloculina*].

Sigmamiliolinella australis (Parr); Loeblich & Tappan 1994, Pl 100, Figs 1-3, Sahul Shelf.

Betjeman (1969) recorded "*Miliolinella australis*" as rare but widespread on the Western Australian shelf.

Sigmoihauerina involuta (Cushman); [*Hauerina*].

Sigmoihauerina involuta (Cushman); Loeblich & Tappan 1994, Pl 100, Figs 8-12, Sahul Shelf.

Sigmoilinella tortuosa Zheng; Figure 4:20,21.

Cycloforina collinsi Langer and *Adelosina pascuaensis* Koutsoukos & Falcetta are probably junior subjective synonyms of *S. tortuosa*.

Sorites marginalis (Lamarck); [Orbulites].

Sorites marginalis (Lamarck); Loeblich & Tappan 1994, Pl 112, Figs 1-5, Sahul Shelf.

Spiroloculina angulata Cushman; Figure 4:22.

Spiroloculina angulata Cushman; Mackenzie 1962, Oyster Harbour.

Quilty (1977) noted this species from Hardy Inlet.

Spiroloculina hadai Thalmann.

Spiroloculina hadai Thalmann; Loeblich & Tappan 1994, Pl 66, Figs 11-15, Sahul Shelf.

Spiroloculina scrobiculata Cushman.

Spiroloculina milletti Wiesner; Mackenzie 1962, pl.2, Fig 4, Oyster Harbour.

Spiroloculina scrobiculata Cushman; Loeblich & Tappan 1994, Pl 67, Figs 12-16, Sahul Shelf.

Spiroloculina subimpressa Parr.

Spiroloculina subimpressa Parr; Loeblich & Tappan 1994, Pl 68, Figs 9-15, Sahul Shelf.

Triloculina barnardi Rasheed; Figure 4:23.

Triloculina littoralis Collins.

Triloculina littoralis Collins; Loeblich & Tappan 1994, Pl 95, Figs 11-13, Sahul Shelf.

Triloculina papuaensis Rasheed; Figure 4:24.

Triloculina tricarinata d'Orbigny; Mackenzie 1962, Oyster Harbour.

T. papuaensis differs from *T. tricarinata* by the presence of a apertural neck.

Triloculina tricarinata d'Orbigny.

Triloculina tricarinata d'Orbigny; Loeblich & Tappan 1994, Pl 96, Figs 1-7, Sahul Shelf.

Bejerman (1969) recorded this species as widespread on the Western Australian shelf.

Triloculina vespertilio Zheng.

Triloculina striatotrigonula Parker & Jones; Quilty 1977, Fig 17, Hardy Inlet.

Triloculina vespertilio Zheng; Loeblich & Tappan 1994, Pl 97, Figs 1-6, Sahul Shelf.

Vertebralina striata d'Orbigny.

Vertebralina striata d'Orbigny; Mackenzie 1962, Pl 1, Fig 20, Oyster Harbour; Loeblich & Tappan 1994, Pl 60, Figs 1-7, Sahul Shelf.

Bejerman (1969) noted this species as common in Cockburn Sound (Rottnest Shelf region).

Wiesnerella auriculata (Egger); [Planispirina].

Wiesnerella auriculata (Egger); Loeblich & Tappan 1994, Pl 62, Figs 1-3, Sahul Shelf.

Order Spirillinida

Conicospirillinoides semidecoratus (Heron-Allen & Earland); [Spirillina].

Conicospirillinoides semidecoratus (Heron-Allen & Earland); Loeblich & Tappan 1994, Pl 50, Figs 1-9, Sahul Shelf.

Conicospirillinoides sp; Figure 5:1,2.

Mychostomina sp; Figure 4:25-27.

Spirillina vivipara Ehrenberg.

Spirillina vivipara Ehrenberg; Loeblich & Tappan 1994, Pl 54, Figs 5-10, Sahul Shelf.

The Exmouth specimens fit within the range of variability shown by Brady's (1884, Pl 85, Figs 1-4) figures.

Order Lagenida

Dentalina sp 1; Figure 5:3.

Dentalina sp 2; Figure 5:4.

Fissurina contusa Parr.

Fissurina contusa Parr; Loeblich & Tappan 1994, Pl 136, Figs 11-16, Sahul Shelf.

Bejerman (1969) noted that this species is more abundant on southern rather than northern sectors of the Western Australian shelf.

Fissurina crassiporosa McCulloch.

Fissurina crassiporosa McCulloch; Loeblich & Tappan 1994, Pl 155, Figs 15,16, Sahul Shelf.

The Western Australian specimens appear closer to the holotype (McCulloch 1977, p. 98, Pl 56, Fig 16) than the paratypes which appear to have a granular rather than smooth surface and lack a distinct basal spine.

Fissurina globosocaudata Albani & Yassini.

Fissurina robusta Zheng; Loeblich & Tappan 1994, Pl 158, Figs 5-8, Sahul Shelf.

F. robusta lacks the basal protrudences of *F. globosocaudata*, and has opaque U-shaped areas on either side of test which are absent in *F. globosocaudata*.

Fissurina sp cf *F. granulocostulata* Zheng.

Cerebrina granulocostata (Zheng); Loeblich & Tappan 1994, Pl 135, Figs 1-7, Sahul Shelf.

The apertural neck in the Western Australian specimens is more extended than in *F. granulocostulata*.

Fissurina lacunata (Burrows & Holland); [Lagena].

Cerebrina lacunata (Burrows & Holland); Loeblich & Tappan 1994, Pl 135, Figs 8-15, Sahul Shelf.

Bejerman (1969) noted that this species is more abundant on southern rather northern sectors of the Western Australian shelf.

Fissurina subquadrata Parr.

Fissurina quadrata (Williamson); Loeblich & Tappan 1994, Pl 155, Figs 1-10, Sahul Shelf.

F. quadrata has a short neck and lacks the marginal groove of *F. subquadrata*.

Fissurina sanpedroensis (McCulloch); [*Lagenosolenia*].

Lagenosolenia sanpedroensis McCulloch; Loeblich & Tappan 1994, Pl 161, Figs 3,4, Sahul Shelf.

Fissurina trinalimarginata (Loeblich & Tappan); [*Duplella*]

Duplella trinalimarginata Loeblich & Tappan 1994, Pl 154, Figs 4-8, Sahul Shelf.

A distinct double slit aperture is not present in the Exmouth specimens and was not shown on Loeblich & Tappan's (1994) figures of the type specimens.

Fissurina wrightiana (Brady); [*Lagena*].

Fissurina wrightiana (Brady); Loeblich & Tappan 1994, Pl 158, Figs 1,2, Sahul Shelf.

Fissurina sp 1; Figure 5:5.

Fissurina sp 2; Figure 5:6.

Glandulina sp cf *G. symmetrica* McCulloch.

Glandulina symmetrica McCulloch; Loeblich & Tappan 1994, Pl 168, Figs 6-8, Sahul Shelf.

The species differs from the bathyal *G. symmetrica* by lacking the series of short diverging spines at the base of the test.

Glandulina sp; Figure 5:7.

Guttulina bartschi Cushman & Ozawa.

Guttulina bartschi Cushman & Ozawa; Loeblich & Tappan 1994, Pl 145, Figs 5-15, Sahul Shelf.

Guttulina regina (Brady, Parker & Jones); [*Polymorphina*].

Guttulina regina (Brady, Parker & Jones); Loeblich & Tappan 1994, Pl 146, Figs 1-3. *Guttulina* sp; Figure 5:8.

Lagena dorbignyi R.W. Jones.

Lagena dorbignyi R.W. Jones; Loeblich & Tappan 1994, Pl 138, Figs 6-9, Sahul Shelf.

Lagena oceanica Albani.

Pygmaeosestron oceanicum (Albani); Loeblich & Tappan 1994, p. 80, Pl 144, Figs 4-7, Sahul Shelf.

Lenticulina domantayi (McCulloch); [*Robulus*].

Lenticulina domantayi (McCulloch); Loeblich & Tappan 1994, Pl 121, Figs 1-8, Sahul Shelf.

Nodosaria catesbyi d'Orbigny.

Pyramidulina catesbyi (d'Orbigny); Loeblich & Tappan 1994, Pl 116, Figs 10-12, Sahul Shelf.

Oolina melosquamosa McCulloch.

Favulina melosquamosa (McCulloch); Loeblich & Tappan 1994, Pl 151, Figs 13-17, Sahul Shelf.

Procerolagena gracillima (Seguenza); [*Amphorina*].

Hyalinonetrion distomapolitum (Parker & Jones); Loeblich & Tappan 1994, Pl 137, Figs 10-12.

Pseudoglandulina sp; Figure 5:9.

Sigmoidella elegantissima (Parker & Jones); [*Polymorphina*].

Sigmoidella elegantissima (Parker & Jones); Mackenzie 1962, Pl 3, Fig 4, Oyster Harbour; Loeblich & Tappan 1994, Pl 148, Figs 4-12, Sahul Shelf.

Webbinella sp; Figure 5:10.

Order Buliminida

Abditodendrix rhomboidalis (Millelt); [*Textularia*].

Tortoplectella rhomboidalis (Millelt); Loeblich & Tappan 1994, Pl 216, Figs 1-6, Sahul Shelf.

Angulogerina sp 1; Figure 5:11.

Angulogerina sp 2; Figure 5:12

Bolivina striatula Cushman; Figure 5:13.

Bolivina vadeszens Cushman.

Bolivina vadeszens Cushman; Loeblich & Tappan 1994, Pl 214, Figs 1-4,7-12, Sahul Shelf.

Bolivina variabilis (Williamson); [*Textularia*].

Bolivina variabilis (Williamson); Loeblich & Tappan 1994, Pl 216, Figs 7-15, Sahul Shelf.

Bolivina sp 1; Figure 5:14.

Bolivina sp 2; Figure 5:15.

Bulimina marginata d'Orbigny.

Bulimina marginata d'Orbigny; Loeblich & Tappan 1994, Pl 242, Figs 1-4, Sahul Shelf.

Buliminoides williamsonianus (Brady); [*Bulimina*].

Buliminoides williamsonianus (Brady); Loeblich & Tappan 1994, Pl 297, Figs 1-9, Sahul Shelf.

Quilty (1977) noted this species in Hardy Inlet. The suprageneric classification of the species is uncertain (Reverts 1990).

Chrysalidinella dimorpha (Brady); [*Chrysalidina*].

Chrysalidinella dimorpha (Brady); Loeblich & Tappan 1994, Pl 252, Figs 7-13, Sahul Shelf.

Elongobula sp cf *E. cochlea* (Wiesner).

Floresina durrandi Reverts; Loeblich & Tappan, Pl 245, Figs 1-6, Sahul Shelf.

Elongobula milletti (Cushman); [*Buliminella*]; Figure 5:16-18.

Evolvocassidulina sp; Figure 5:19.

Fursenkoia pauciloculata (Brady); [*Virgulina*].

Fursenkoia pauciloculata (Brady); Loeblich & Tappan 1994, Pl 256, Figs 1-5, Sahul Shelf.

The Exmouth specimens differ from typical *F. pauciloculata* in having a few more chambers in the adult test.

Globocassidulina sp; Figure 5:20.

Hopkinsinella glabra (Millelt); [*Uvigerina*].

Hopkinsinella glabra (Millelt); Loeblich & Tappan, Pl 232, Figs 1-11, Sahul Shelf.

Loxostomina costatapertusa Loeblich & Tappan.

Loxostomina costatapertusa Loeblich & Tappan 1994, Pl 234, Figs 1-12, Sahul Shelf.

Loxostomina costulata (Cushman); [*Bolivina*].

Loxostomina costulata (Cushman); Loeblich & Tappan 1994, Pl 232, Figs 12-16, Sahul Shelf.

This identification follows the interpretation of Hottinger *et al.* (1993) who showed a range of ornament from a few costae (as in Cushman's type) to numerous costae over the entire test.

Loxostomina limbata (Brady); [*Bolivina*].

Loxostomina limbata (Brady); Loeblich & Tappan 1994, Pl 233, Figs 1-8, Sahul Shelf.

Specimens with few faint costae over the initial part of test are transitional to *L. costulata*.

Millettia limbata (Brady); [*Sagrina*].

Millettia limbata (Brady); Loeblich & Tappan, Pl 255, Figs 7-8, Sahul Shelf.

Neocassidulina abbreviata (Heron-Allen & Earland); [*Bolivina*].

Neocassidulina abbreviata (Heron-Allen & Earland); Loeblich & Tappan 1994, p.131, Pl 258, Figs 1-7, Sahul Shelf.

This species is synonymous with *Bolivina makiyamae* Ishizaki. Haig (1993) suggested that transitional morphotypes may exist between *N. abbreviata* and *Neocassidulina capitata* (Cushman). Although *N. capitata* has not been found in Exmouth Gulf, morphotypes of *N. abbreviata* trending toward the more inflated, more loosely embracing chamber arrangement of *N. capitata* are present.

Neouvigerina ampullacea (Brady); [*Uvigerina*].

Neouvigerina ampullacea (Brady); Loeblich & Tappan 1994, Pl 246, Figs 9-19, Sahul Shelf.

Radiatobolivina okinawacensis Hatta.

Radiatobolivina okinawacensis Hatta in Hatta & Ujiie 1992, p. 205-206, Pl 51, Figs 1a-2c, 3-5.

Krebsina subtenuis (Cushman); Loeblich & Tappan 1994, Pl 146, Figs 12-16; Sahul Shelf.

Radiatobolivina sp.

Krebsina pilasensis (McCulloch); Loeblich & Tappan 1994, Pl 146, Figs 10,11.

The relationship of *Krebsina* McCulloch to *Radiatobolivina* Hatta is uncertain, as is the suprageneric classification of these taxa.

Reussella sp 1; Figure 5:21.

Reussella sp 2; Figure 5:22

Reussella sp 3; Figure 5:23-25.

Rugobolivina elegans (Parr); [*Bolivina*].

Rugobolivina elegans (Parr); Loeblich & Tappan 1994, Pl 220, Figs 1-6, Sahul Shelf.

Bejerman (1969) noted the species (as *Bolivina elegans*) from Exmouth Gulf and the Rowley Shelf.

Sagrinea jugosa (Brady); [*Textularia*].

Sagrinea jugosa (Brady); Loeblich & Tappan 1994, Pl 237, Figs 12-17, Sahul Shelf.

The generic attribution follows Revets (1996).

Sagrinea sp.

Sagrinea zanzibarica (Cushman); Loeblich & Tappan 1994, Pl 238, Figs 12-17, Sahul Shelf.

The species differs from *Bolivina zanzibarica* Cushman in apertural details (having a high-arched aperture without projecting toothplate in contrast to an elliptical aperture with distinct raised lip) and in having more inflated, less angulate adult chambers.

Sagrinea scutata Saidova.

Sagrinea scutata Saidova; Loeblich & Tappan 1994, Pl 236, Figs 9, 10, Sahul Shelf.

The generic attribution is uncertain. Haig (1993) included similar morphotypes in "*Sagrinea*" gr. *convallarium* (Millett); however, the apparent broad range of variability recorded in the Papuan assemblage is not present among the Exmouth Gulf specimens.

Sagrinea fimbriata (Millett); [*Bigenerina*].

Sagrinea fimbriata (Millett); Loeblich & Tappan 1994, Pl 239, Figs 1-10, Sahul Shelf.

Sigmavirgulina tortuosa (Brady); [*Bolivina*].

Sigmavirgulina tortuosa (Brady); Loeblich & Tappan 1994, Pl 261, Figs 1-10, Sahul Shelf.

Bejerman (1969) noted this species is more abundant on southern sectors of the Western Australian shelf.

Siphogenerina raphana (Parker & Jones); [*Uvigerina*].

Siphogenerina raphana (Parker & Jones); Mackenzie 1962, Oyster Harbour; Loeblich & Tappan 1994, Pl 240, Figs 1-3, 4-5, 6-11, Sahul Shelf.

Quilty (1977) noted the species (as *Rectobolivina raphanus*) in Hardy Inlet.

Siphouvigerina porrecta (Brady); [*Uvigerina*].

Siphouvigerina porrecta (Brady); Loeblich & Tappan, Pl 247, Figs 6-11, Sahul Shelf.

Valvobifarina mackinnoni (Millett); [*Bifarina*].

Valvobifarina mackinnoni (Millett); Loeblich & Tappan 1994, Pl 254, Figs 9-12, Sahul Shelf.

Order Rotaliida

Aceroulina mahabeti (Said); [*Planorbulina*]; Figure 5:26.

Planorbulina aceroulis Brady; Mackenzie 1962, Pl 3, Fig 16, Oyster Harbour.

The identification of this species follows Hottinger *et al.* (1993, p. 122,123, Pl 165, Figs 1-7, Pl 166, Figs 1-8). The specimen figured by Loeblich & Tappan (1994, Pl 323, Figs 11-13) may be a juvenile of the species.

Ammonia parkinsoniana (d'Orbigny); [*Rosalina*].

Ammonia parkinsoniana (d'Orbigny); Loeblich & Tappan 1994, Pl 368, Figs 7-16; Sahul Shelf.

? *Streblus beccarii* (Linné); Mackenzie 1962, Pl 3, Fig 18, Oyster Harbour.

Ammonia supera Belford.

Ammonia supera Belford; Loeblich & Tappan 1994, Pl 370, Figs 7-9, Sahul Shelf.

Ammonia sp; Figures 5:27, 6:1.

This seems to be the same form illustrated by Loeblich & Tappan (1994, Pl 387, Figs 4-6) as *Notorotalia inornata* Vella. Unlike Vella's types, the Exmouth specimens have an open umbilicus and some (e.g. Fig 5:27) have a prominent umbonal plug. A peripheral keel, prominent in *N. inornata*, is absent in the Western Australian species.

Amphistegina lessonii d'Orbigny.

Amphistegina lessonii d'Orbigny; Loeblich & Tappan 1994, Pl 340, Figs 1-9, Sahul Shelf.

Betjeman (1969) noted this species as widespread on the Western Australian shelf, and Quilty (1977) recorded it from Hardy Inlet.

Amphistegina sp cf *A. papillosa* Said.

Amphistegina papillosa Said; Loeblich & Tappan 1994, Pl 339, Figs 4-7; Pl 341, Figs 1-7, Sahul Shelf.

The Western Australian specimens are generally smaller and do not have the intensity of ornament shown by the type specimen. Betjeman (1969) recorded "*Amphistegina radiata* var. *papillosa*" from Shark Bay and areas north on the Western Australian shelf.

Amphistegina radiata (Fichtel & Moll); [*Nautilus*].

Amphistegina radiata (Fichtel & Moll); Loeblich & Tappan 1994, Pl 339, Figs 8-11, Pl 341, Figs 8-10.

Angulodiscorbis corrugatus (Millett); [*Discorbina*]

Angulodiscorbis corrugatiformis (McCulloch); Loeblich & Tappan 1994, Pl 290, Figs 8-10, Sahul Shelf.

Anomalinulla glabrata (Cushman); [*Anomalina*]; Figure 6:2,3.

Anomalinoides globulosa (Chapman & Parr); Loeblich & Tappan 1994, Pl 355, Figs 4-5, 10-13 (not Figs 7,8; not Pl 354, Figs 11-12).

Asanonella tubulifera (Heron-Allen & Earland); [*Truncatulina*].

Asanonella tubulifera (Heron-Allen & Earland); Loeblich & Tappan 1994, Pl 337, Figs 1-10, Sahul Shelf.

Ashbrookia ornata McCulloch.

Ashbrookia tuberculata Ujiié; Loeblich & Tappan 1994, Pl 262, Figs 1-3, Sahul Shelf.

The Western Australian specimens lack the distinct radial grooves around the aperture that characterise *A. tuberculata*; and have the matte granular surface of the spiral side of *A. ornata*.

Asterorotalia gaimardi (d'Orbigny); [*Turbinulina*].

Asterorotalia gaimardi (d'Orbigny); Loeblich & Tappan 1994, Pl 372, Figs 1-7, Sahul Shelf.

Astrononion sp; Figure 6:4,5.

Baggina bubnanensis McCulloch.

Baggina bubnanensis McCulloch; Loeblich & Tappan, Pl 264, Figs 5-10, Sahul Shelf.

Cancris auriculus (Fichtel & Moll); [*Nautilus*].

Cancris auriculus (Fichtel & Moll); Loeblich & Tappan 1994, Pl 265, Figs 7-10, Sahul Shelf.

The specimens figured by Loeblich & Tappan (1994, Pl 266, Figs 1-13) as *C. carinatus* (Millett) may belong to this species; they lack the triangular cross-section in the last chamber that is characteristic of Millett's species.

Caribbeanella sp cf *C. ogiensis* (Matsunaga); [*Oinonikadoina*].

Caribbeanella ogiensis (Matsunaga); Loeblich & Tappan 1994, Pl 325, Figs 1-10, Sahul Shelf.

In contrast to the types of *C. ogiensis*, the Western Australian specimens maintain an angulate margin in the adult stage and have a more lobulate periphery in the last few chambers. *Caribbeanella elatensis* Perelis & Reiss has a thicker test.

Caribbeanella philippinensis McCulloch.

Caribbeanella philippinensis McCulloch; Loeblich & Tappan 1994, Pl 324, Figs 1-9, Sahul Shelf.

Cibicides sp cf *C. refulgens* Montfort.

Cibicides refulgens Montfort; Mackenzie 1962, Pl 3, Fig 33, Oyster Harbour; Quilty 1977, Figs 42,43, Hardy Inlet; Loeblich & Tappan 1994, Pl 318, Figs 7-9, Sahul Shelf.

The Western Australian specimens have 9-10 chambers in the final whorl in contrast to 6 chambers in *C. refulgens*. The sutures on the umbilical side tend to be limbate, and the umbilical shoulder of the final chamber tends to be elevated above the shoulders of previous chambers. Betjeman (1969) noted that "*Cibicides refulgens*" is common and widespread on the Western Australian shelf.

?*Cibicides* sp; Figure 6:6-8.

A relationship between this species and *Pulvinulina corticata* Heron-Allen & Earland is suspected.

Cibicidoides basilanensis McCulloch; Figure 6:9,10.

An opaline sheen on the spiral side is a feature of the Exmouth specimens and McCulloch's (1977, p. 445, Pl 187, Figs 1,2) types housed at the Smithsonian Institution, Washington.

Cibicidoides sp; Figure 6:11,12.

Colonimilesia obscura McCulloch.

Colonimilesia obscura McCulloch; Loeblich & Tappan 1994, Pl 282, Figs 1-6, 13-14, Sahul Shelf.

Criobrobaggina socorroensis McCulloch; Figure 6:13,14.

Cymbaloporella tabellaeformis (Brady); [*Cymbalopora*]; Figure 6:15,16.

Cymbaloporetta bradyi (Cushman); [*Cymbalopora*].

Cymbaloporetta bradyi (Cushman); Mackenzie 1962, Oyster Harbour; Loeblich & Tappan 1994, Pl 328, Figs 1-3, Sahul Shelf.

Betjeman (1969) recorded this species as more abundant in northern sectors of the Western Australian shelf.

Discorbinella bodjongensis (Le Roy); [*Discorbis*].

Discorbinella bodjongensis (Le Roy); Loeblich & Tappan 1994, Pl 310, Figs 1-13, Sahul Shelf.

Discorbinella rhodiensis (Terquem); [*Truncatulina*]; Figure 6:17,18.

The identification follows Hottinger *et al.* (1993, p. 115, Pl 150, Figs 5-9).

Discorbinoides patelliformis (Brady); [*Discorbina*].

Discorbinoides minogasisiformis Ujiié; Loeblich & Tappan 1994, Pl 291, Figs 1-10, Sahul Shelf.

The Western Australian specimens lack strong ornament on the spiral side. The specimens from Hardy Inlet that Quilty (1977, Figs 38,39) attributed to this species, do not belong here.

Elphidium sp cf *E. advenum* (Cushman); [*Polystomella*]; Figure 6:19,20.

The Exmouth specimens differ from the specimens illustrated as *E. advenum* by Loeblich & Tappan (1994, Pl 379, Figs 1-4) in having a larger number of chambers

in the final whorl, and more prominent retral processes across the sutures. The Exmouth specimens differ from Oyster Harbour types included in *E. advenum* by Mackenzie (1962) in having slightly fewer chambers in the final whorl and a sharper periphery, and from a specimen figured by Quilty (1977, Fig 54) in having fewer chambers in the adult whorl.

Elphidium albanii Hayward; Figure 6:21,22.

Elphidium albanii Hayward 1997, p. 70,71, Pl 6, Figs 1-5.

Elphidium carteri Hayward.

Elphidium carteri Hayward 1997, p. 71,72, Pl 1, fig.15, Pl 6, Figs 8-12.

Elphidium jenseni (Cushman); Loeblich & Tappan 1994, Pl 381, Figs 4,5, ?1-3, Sahul Shelf.

E. jenseni has more chambers in the adult whorl (around 17) than has *E. carteri* (12-14).

Elphidium sp cf *E. craticulatum* (Fichtel & Moll); [Nautilus]; Figure 6:23.

This species belongs to the group of *Elphidium craticulatum* (Fichtel & Moll), but differs from typical specimens by having interconnected vermiform ridges crossing the broad central umbo.

Elphidium crispum (Linné); [Nautilus].

Elphidium crispum (Linné); Mackenzie 1962, Pl 3, Fig 21, Oyster Harbour; Quilty 1977, Fig 55, Hardy Inlet; Loeblich & Tappan 1994, Pl 378, Figs 4-6, Sahul Shelf.

Bejerman (1969) recorded this species as widespread on the Western Australian shelf.

Elphidium mortonbayensis Albani & Yassini; Figure 6:24,25.

Elphidium mortonbayensis Albani & Yassini 1993, p. 30, Figs 74, 78.

The Exmouth specimens have a more broadly rounded periphery than in the type specimens.

Elphidium neosimplex McCulloch.

Elphidium neosimplex McCulloch; Loeblich & Tappan 1994, Pl 381, Figs 6-11, Sahul Shelf.

Elphidium oceanicum Cushman; Figure 6:26,27.

This is probably the same form as Albani & Yassini (1993, p. 21, Figs 27,28) recorded as *Cribrononion schmitti* (Cushman & Wickenden). The species has a greater number of chambers in the final whorl, and a greater number of more distinct retral processes crossing the sutures than has *C. schmitti*.

Elphidium simplex Cushman.

Elphidium simplex Cushman; Loeblich & Tappan 1994, Pl 385, Figs 1-12, Sahul Shelf.

Bejerman (1969) noted that *E. simplex* occurs from Shark Bay north on the Western Australian shelf. Quilty (1977) recorded the species much further south in Hardy Inlet.

Elphidium sp cf *E. striatopunctatus* (Fichtel & Moll); [Nautilus]; Figure 7:1,2.

Elphidium sp 1; Figure 7:3.

Eupatellinella fastidiosa (McCulloch); [Patellinella].

Eupatellinella fastidiosa (McCulloch); Loeblich &

Tappan 1994, Pl 262, Figs 4-11, Pl 263, Figs 1-6, Sahul Shelf.

Some doubt exists as to the specific identity of the Western Australian specimens. The Exmouth specimens have a keeled margin with the keels of earlier chambers forming low ridges at the chamber contacts on the conical spiral surface. McCulloch (1977, p. 283) described the spiral surface of *E. fastidiosa* as smooth.

Gavelinopsis praegeri (Heron-Allen & Earland); [Discorbina].

Gavelinopsis praegeri (Heron-Allen & Earland); Loeblich & Tappan 1994, Pl 281, Figs 1-10, Sahul Shelf.

Glabratella sp; Figure 7:4,5.

?*Haynesina* sp; Figure 7:6,7.

Heterolepa subhaidingeri (Parr); [Cibicides].

Heterolepa subhaidingeri (Parr); Loeblich & Tappan 1994, Pl 359, Figs 1-13, Sahul Shelf.

Heterostegina depressa d'Orbigny.

Heterostegina depressa d'Orbigny; Loeblich & Tappan 1994, Pl 389, Figs 1-6, Pl 390, Figs 1-3, Sahul Shelf.

Homotrema rubrum (Lamarck); [Millepora].

Homotrema rubrum (Lamarck) [Millepora]; Loeblich & Tappan 1994, Pl 335, Figs 1-4, Sahul Shelf.

Lamellogdiscorbis melbyae Hansen & Revets; Figure 7:8,9.

Lamellogdiscorbis melbyae Hansen & Revets 1992, Pl 4, Figs 4-6, 9.

Discorbis dimidiatus (Jones & Parker) var. *acervulinoides* Parr; Mackenzie 1962, Pl 3, Fig 9, Oyster Harbour.

Discorbis dimidiatus (Jones & Parker); Quilty 1977, Figs 31,32, Hardy Inlet.

?*Melonis* sp.

Anomalinoidea globulosus (Chapman & Parr); Loeblich & Tappan 1994, Pl 354, Figs 11-13, Pl 354, Figs 11-13, Pl 355, Figs 7-9 (not Figs 4,5,10-13).

Millettiana millettii (Heron-Allen & Earland); [Cymbalopora].

Millettiana millettii (Heron-Allen & Earland); Loeblich & Tappan 1994, Pl 329, Figs 1-12, Sahul Shelf.

Miniacina miniacea (Pallas); [Millepora].

Miniacina miniacea (Pallas); Loeblich & Tappan 1994, Pl 335, Figs 5-6, Sahul Shelf.

Monspeliensisina sp 1.

Ammonia convexa (Collins); Loeblich & Tappan 1994, Pl 369, Figs 1-10, Sahul Shelf.

A. convexa has a prominent umbonal plug and lacks the sutural clefts of *Monspeliensisina*.

Monspeliensisina sp 2; Figure 7:10,15.

Murrayinella murrayi (Heron-Allen & Earland); [Rotalia]; Figure 7:11-12.

Most of the specimens figured by Loeblich & Tappan (1994, Pl 293, Figs 1-10) seem atypical of this species.

Neoconorbina terquemi (Rzehak); [Discorbina].

Neoconorbina terquemi (Rzehak); Loeblich & Tappan 1994, Pl 284, Figs 1-12, Sahul Shelf.

Betjeman (1969) recorded the species as more abundant on northern sectors of the Western Australian shelf. Quilty (1977) noted it from Hardy Inlet.

Neorotalia calcar (d'Orbigny); [*Calcarina*]; Figure 7:13,14.

Betjeman (1969) recorded "*Calcarina calcar*" from the Abrolhos Islands and areas north on the Western Australian shelf.

Nonion sp cf *N. subturgidum* (Cushman); [*Nonionina*].

Nonion subturgidum (Cushman); Loeblich & Tappan 1994, Pl 343, Figs 1-9, Sahul Shelf.

The Western Australian species has a greater number of chambers (11-12) in the adult whorl than has *N. subturgidum* (8-9).

Nonionoides sp; Figure 7:16-18.

Nummulites venosus (Fichtel & Moll); [*Nautilus*].

Nummulites venosus (Fichtel & Moll) [*Nautilus*]; Loeblich & Tappan 1994, Pl 388, Figs 5-9, Sahul Shelf.

Betjeman (1965) recorded "*Operculinella venosa*" as more abundant on northern rather than southern sectors of the Western Australian shelf.

Operculina ammonoides (Gronovius); [*Nautilus*].

Assilina ammonoides (Gronovius); Loeblich & Tappan 1994, Pl 387, Figs 7-9, Pl 388, Figs 1-4, Sahul Shelf.

Operculina heterosteginoides Hofker.

Operculina heterosteginoides Hofker; Loeblich & Tappan 1994, Pl 390, Fig 4, Sahul Shelf.

Orbitina carinata Sellier de Civrieux.

Orbitina carinata Sellier de Civrieux; Loeblich & Tappan 1994, Pl 275, Figs 7-12, Sahul Shelf.

Pararotalia nipponica (Asano); [*Rotalia*]; Figure 7:19,20.

Calcarina calcar d'Orbigny; Quilty 1977, Figs 52,53, Hardy Inlet.

The species identification follows Ujiie (1966) who placed spinose *Rotalia ozaawai* Asano into synonymy with *P. nipponica*.

Planogypsina acervalis (Brady); [*Planorbulina*]; Figure 7:21.

Planorbulinella larvata (Parker & Jones); [*Planorbulina*].

Planorbulinella larvata (Parker & Jones); Mackenzie 1962, Pl 3, Fig 17, Oyster Harbour; Loeblich & Tappan 1994, Pl 327, Figs 1-7, Sahul Shelf.

Poroceponides lateralis (Terquem); [*Rosalina*]; Figure 7:22.

The Sahul Shelf specimens figured by Loeblich & Tappan (1994, Pl 269, Figs 1-9) as *Eponides cribreropandus* (Asano & Uchio) belong to *P. lateralis* as recognized by Hottinger *et al.* (1991). The figured Exmouth specimen represents an end member of the *P. lateralis* plexus.

Rosalina cosymbosella Loeblich & Tappan 1994.

Rosalina cosymbosella Loeblich & Tappan 1994, p. 140, Pl 287, Figs 1-3, Sahul Shelf.

Rosalina globularis d'Orbigny.

Rosalina globularis d'Orbigny; Loeblich & Tappan 1994, Pl 286, Figs 7-15, Sahul Shelf.

Rotorbis auberi (d'Orbigny); [*Rosalina*].

Discorbis mira Cushman; Mackenzie 1962, Pl 3, Fig 10, Oyster Harbour.

Rotorbis auberi (d'Orbigny); Loeblich & Tappan 1994, Pl 278, Figs 1-8, 9-11, Sahul Shelf.

Betjeman (1969) recorded "*Discorbis mira*" as a widespread although rare species on the Western Australian shelf.

?*Saintclairoides* sp; Figure 7:23,24.

The generic designation is tentative. Loeblich & Tappan (1987) provisionally placed *Saintclairoides* McCulloch among the ceratobulimines (Order Robertinida), and suggested that the systematic position of the genus depended on additional information regarding the aperture and internal features of the test. The Exmouth specimen appears to lack an internal partition.

Schwartzia sp; Figure 7:25,26.

Siphonina tubulosa Cushman.

Siphonina tubulosa Cushman; Loeblich & Tappan 1994, Pl 299, Figs 1-10, Sahul Shelf.

Siphoninoides laevigatus (Howchin); [*Truncatulina*].

Siphoninoides laevigatus (Howchin); Loeblich & Tappan 1994, Pl 300, Figs 1-4, Sahul Shelf.

Sphaerogypsina globula (Reuss); [*Ceripora*].

Gypsina globulus (Reuss); Quilty 1977, Fig 60, Hardy Inlet.

Sphaerogypsina globula (Reuss); Loeblich & Tappan 1994, Pl 334, Figs 4-6, Sahul Shelf.

Stomatorbina concentrica (Parker & Jones); [*Pulvinulina*].

Stomatorbina concentrica (Parker & Jones); Loeblich & Tappan 1994, Pl 273, Figs 1-7, Sahul Shelf.

Quilty (1977) noted this species, as *Mississippina concentrica*, from Hardy Inlet.

Order Globigerinida

Globigerinoides ruber (d'Orbigny); [*Globigerina*].

Globigerinoides ruber (d'Orbigny); Loeblich & Tappan 1994, Pl 203, Figs 1-9, Pl 206, Figs 10-12, Sahul Shelf.

Globigerinoides trilobus (Reuss); [*Globigerina*].

Globigerinoides trilobus (Reuss); Loeblich & Tappan 1994, Pl 206, Figs 1-6, Sahul Shelf.

Globorotalia menardii (Parker, Jones & Brady); [*Rotalia*].

Globorotalia menardii (Parker, Jones & Brady); Loeblich & Tappan 1994, Pl 183, Figs 1-6.

Globoturborotalita rubescens (Hofker); [*Globigerina*].

Globoturborotalita rubescens (Hofker); Loeblich & Tappan 1994, Pl 208, Figs 1-12, Sahul Shelf.

Neogloboquadrina humerosa (Takayanagi & Saito); [*Globorotalia*].

Neogloboquadrina humerosa (Takayanagi & Saito); Loeblich & Tappan 1994, Pl 199, Figs 1-6, Sahul Shelf.

Tinophodella ambitacrena Loeblich & Tappan.

Tinophodella ambitacrena Loeblich & Tappan; Loeblich & Tappan 1994, Pl 192, Figs 1-9, Pl 200, Figs 1-6, Sahul Shelf.

Table 1.

Distributions of major foraminiferal groups and those species present in at least one sample at frequencies <5% . Abundances are given as percentages in systematic foraminiferal counts from the 150 µm - 2 mm sediment fraction.

SAMPLES	Planktonic Foraminifera	Benthonic Groups	Agglutinated	Porcellaneous	Hyaline (Lagenida)	Hyaline (Buliminida)	Hyaline (Rotaliida)	Agglutinated species	<i>Ammonitium australiensis</i>	<i>Textularia foliacea</i>	<i>Textularia oceanica</i>	<i>Textularia lateralis</i>	Porcellaneous species	<i>Parahauenerioides fragillissimus</i>	<i>Peneroplis portusius</i>	<i>Planispirinella exigua</i>	<i>Pseudomassilina australis</i>	<i>Quinqueloculina arenata</i>	<i>Quinqueloculina philippinensis</i>	<i>Quinqueloculina</i> sp 8	<i>Signolhuerna involuta</i>	<i>Sorites marginalis</i>	<i>Triloculina tricarinata</i>	Hyaline species - Rotaliida	<i>Ammonia parkinsoniana</i>	<i>Amphistegina lessonii</i>	<i>Amphistegina</i> sp cf <i>A. pupillosa</i>	<i>Amphistegina radiata</i>	<i>Asterorotalia gainardi</i>	<i>Cibicides</i> sp cf <i>C. refulgens</i>	<i>Discorinoides patelliformis</i>	<i>Elphidium crispum</i>	<i>Elphidium</i> sp cf <i>E. advenum</i>	<i>Elphidium</i> sp 1	<i>Heterostegina depressa</i>	<i>Operculina ammonoides</i>	<i>Pararotalia nipponica</i>	<i>Rosalina cosymbosella</i>
996	2	7	53	1	3	36		0	0	0	0		4	1	0	1	2	3	1	2	1	0		5	4	0	0	0	7	2	0	1	0	0	2	1	0	
999	0	4	55	1	4	36		0	0	2	1		2	8	2	1	0	0	2	6	1	1		0	1	1	0	0	0	6	1	0	0	0	1	3	0	
1002	0	3	53	1	0	42		0	0	1	0		1	10	1	1	3	1	0	1	0	1		0	7	4	0	0	0	10	1	1	2	1	0	10	0	
1004	0	6	55	0	1	38		1	0	1	2		2	10	5	1	1	0	1	10	3	3		0	4	3	0	0	0	9	1	2	0	0	0	5	1	
1006	0	5	50	1	0	45		0	1	2	1		1	13	2	1	0	2	0	1	2	1		1	4	1	0	0	0	6	3	2	2	1	1	11	0	
1008	0	5	60	0	1	33		1	0	1	1		0	12	1	1	2	1	2	3	2	5		0	1	1	0	0	0	7	1	1	0	1	1	8	2	
1010	1	10	56	2	4	27		0	0	3	5		0	3	2	0	1	5	7	2	0	2		0	3	2	0	1	0	1	1	2	1	0	2	0	1	
1012	0	1	66	1	1	32		0	0	1	0		2	10	5	1	1	2	0	7	1	0		0	0	1	0	0	0	3	2	2	1	1	9	1		
1015	1	11	49	0	1	39		1	0	3	0		2	3	3	0	2	3	4	4	0	6		4	0	1	0	0	0	6	2	2	1	2	1	7	0	
1017	1	5	42	2	2	49		0	1	3	0		0	7	4	1	3	1	0	1	1	1		0	6	6	0	1	1	6	4	1	0	8	1	5	1	
1021	2	8	41	1	4	47		0	1	2	2		2	5	4	1	1	0	1	2	2	2		0	3	3	0	1	2	0	1	1	0	2	0	2	3	
1023	1	4	33	0	7	57		0	0	2	0		3	7	2	1	0	3	1	1	0	0		0	3	0	0	0	8	3	4	1	3	1	3	4	0	
1024	2	4	36	1	5	53		0	0	1	1		0	4	1	0	1	1	2	1	1	1		1	5	3	0	0	7	1	5	1	4	1	2	3	0	
1027	0	4	12	1	2	81		0	0	1	2		0	2	0	0	0	0	0	0	1	0		0	21	6	21	0	3	0	3	0	6	3	1	0	0	
1029	0	13	43	0	0	44		0	3	1	3		0	11	2	2	4	6	0	0	0	2		0	3	3	0	1	4	0	11	3	4	1	2	3	0	
1031	0	17	38	1	2	43		0	0	7	4		1	6	1	2	3	4	1	0	1	1		0	6	10	0	2	3	0	6	3	3	1	1	1	0	
1033	0	9	33	4	1	53		0	1	1	6		0	5	0	1	3	6	0	0	0	1		0	6	6	0	0	4	0	16	2	2	0	1	0	0	
1035	0	5	48	0	1	46		0	0	1	3		1	12	2	4	1	3	0	1	0	1		0	3	4	0	0	4	0	15	3	3	1	1	0	1	
1040	0	8	38	1	2	52		0	1	3	3		3	7	0	1	0	3	1	0	2	3		0	8	5	0	1	1	1	2	0	0	6	1	5	1	
1042	0	19	48	0	7	34		0	1	6	4		1	4	2	1	2	1	1	4	2	3		0	1	1	0	4	1	1	0	1	1	1	1	4	1	
1044	0	11	55	0	4	28		0	2	2	6		3	8	5	4	0	0	2	3	1	3		0	1	1	0	1	0	3	0	2	0	2	0	1	2	
1048	0	8	41	1	5	45		0	1	1	5		1	1	1	1	0	0	1	1	3	4		4	0	0	0	0	0	12	0	1	0	2	0	0	4	
1050	1	30	44	1	0	26		0	2	10	6		0	7	1	1	3	6	0	1	1	1		0	6	3	0	0	1	0	0	3	3	1	0	0	1	
1052	1	6	66	0	0	27		0	0	3	1		2	18	3	2	5	0	0	5	1	0		2	0	0	1	0	5	0	5	0	3	2	0	5	1	
1053	0	12	47	0	3	38		0	3	4	3		1	5	8	2	0	0	1	1	4	3		3	2	0	0	3	1	3	0	3	1	1	0	6	0	
1054	0	11	41	0	4	51		0	1	6	3		3	4	5	4	0	0	1	1	1	0		2	0	1	0	2	1	7	1	1	1	0	0	3	0	
1056	0	14	45	1	3	37		2	2	6	1		2	2	3	1	1	0	0	2	3	2		1	1	0	0	0	0	5	0	2	0	2	0	3	1	
1058	0	24	38	1	2	35		0	2	8	4		1	4	4	4	0	4	0	1	2			1	0	0	0	4	1	1	0	1	0	0	6	1	1	
1060	0	18	42	3	3	34		0	3	10	4		1	4	2	0	3	8	0	0	1	2		0	1	2	0	2	1	1	0	0	2	1	2	0	1	
1062	1	8	54	0	2	36		0	3	1	2		2	12	2	2	0	1	5	0	0	0		0	0	3	0	0	0	5	0	1	3	0	1	11	1	
1064	0	23	48	0	1	29		0	2	9	7		1	8	2	2	5	7	0	2	0	1		0	2	2	0	2	2	1	0	5	5	0	1	1	2	
1066	0	22	50	0	2	26		0	1	12	5		1	9	5	3	3	5	1	2	0	1		1	2	3	0	2	1	1	0	1	3	2	1	1	1	
1067	1	12	50	0	5	32		1	1	6	3		3	10	3	4	2	4	0	4	1	0		1	3	2	0	0	0	5	1	2	6	1	0	2	0	
1068	0	13	49	0	2	37		0	0	6	3		0	16	2	0	0	3	1	0	0	3		0	6	3	0	0	0	2	1	0	2	3	0	1	2	
1069	0	12	60	1	1	27		0	0	6	2		1	10	5	2	2	6	2	1	0	3		0	0	4	0	2	0	0	2	4	0	2	0	2	0	0
1070	1	26	42	1	2	29		0	9	9	3		2	6	2	3	1	3	0	0	0	3		1	1	1	0	1	0	2	0	0	1	0	1	1	0	
1071	0	5	72	1	0	23		0	1	1	3		1	20	1	0	0	3	0	7	0	1		0	0	0	0	0	0	7	1	2	1	0	0	3	1	
1073	0	2	68	0	0	29		0	0	0	1		0	22	0	1	0	2	0	1	0	0		0	8	1	0	0	0	2	2	0	3	1	0	3	1	
1075	0	17	46	2	2	32		0	3	7	2		2	2	2	3	2	2	1	0	2	6		2	1	1	0	7	0	2	0	1	2	0	1	1	0	
1078	1	21	50	0	1	28		0	2	10	3		0	6	8	3	1	2	0	0	3	4		2	0	1	0	3	0	1	0	2	2	0	0	1	0	
1080	1	5	51	1	4	39		0	2	2	1		2	4	12	2	0	2	2	2	3	0		2	0	0	0	5	0	4	0	0	2	2	0	4		
1082	0	13	51	0	0	36		0	5	6	0		0	6	18	4	0	3	2	0	1	2		2	1	0	0	5	0	6	0	1	2	2	1	3	0	
1083	0	11	55	0	0	34		0	0	5	3		1	22	1	0	2	2	0	0	0	0		0	0	4	0	1	0	1	2	0	7	1	2	1	0	
1085	0	7	55	0	0	37		0	0	3	2		2	6	11	4	0	0	0	1	2	3		2	1	1	0	0	0	2	0	2	0	2	0	1	4	2
1090	0	3	71	1	0	26		0	0	1	0		3	12	13	1	2	0	2	3	1	0		5	0	0	0	0	0	1	1	1	0	0	0	3	2	
1091	0	3	69	0	0	29		0	0	1	2		0	34	1	0	1	1	0	0	0	0		1	5	0	0	1	0	2	9	1	7	0	0	1	0	
1093	0	4	63	0	2	32		0	1	0	2		2	9	15	4	0	1	2	2	0	1		4	0	0	0	0	0	4	0	0	2	0	1	6	2	
1095	0	5	49	1	3	42		0	0	2	2		2	6	8	2	2	1	0	2	1	0		1	9	8	0	0	0	4	1	1	0	2	0	7	0	
1097	0	16	49	0	1	34		0	5	8	3		3	5	14	3	0	0	1	0	1	1		1	0	1	0	5	0	4	0	1	0	1	0	1	1	
1099	1	19	33	0	3	45		0	4	6	1		0	2	3	2	0	1	1	3	1	1		1	0	0	0	3	0	7	0	0	2	0	0	0	3	

Discussion

The identified microfauna is composed of 242 species, including 236 benthonic taxa (comprising 20 agglutinated, 74 porcellaneous, and 142 hyaline types). Six planktonic species are also present. In terms of abundance (Table 1), the porcellaneous species dominate and, with the hyaline Rotaliida, they form the bulk of the foraminiferal assemblages. Most of the species are very rare and sporadic within gulf sediments. Four agglutinated species, ten porcellaneous species, and 14 hyaline rotaliid species are present at frequencies >5% of the total foraminiferal count in the 150 µm - 2 mm sediment fraction (Table 1).

Because of lack of similar taxonomic databases for other areas along the western coast of Western Australia, only limited biogeographic comparisons can be drawn at present. In comparison with the shallow-marine microfauna from the Sahul Shelf recorded by Loeblich & Tappan (1994), unusual occurrences in Exmouth Gulf which may have biogeographic significance include; (1) the presence of *Borelis schlumbergeri* not recorded from the Sahul Shelf, and the absence of related *Alveolinella quoyi* (d'Orbigny) which was recorded from the Sahul Shelf; (2) the absence of *Calcarina* which is represented by several species on the Sahul Shelf; (3) the absence of *Baculogypsinoidea* present on the Sahul Shelf; and (4) the presence of *Neorotalia calcar* not recorded from the Sahul Shelf, and the absence of *Pararotalia domantayi* McCulloch (often misidentified as *Calcarina calcar* d'Orbigny) which is present on the Sahul Shelf.

A major foraminiferal habitat that is rare in Exmouth Gulf is the seagrass meadow. McCook *et al.* (1995) recorded low abundances of seagrasses in the Gulf, and attributed this to the lack of suitable substrates. The lack of seagrass beds is reflected in the foraminiferal assemblages by the very low abundance of the porcellaneous "larger" Foraminifera, *Amphisorus hemprichii*, which is an abundant epiphytic species elsewhere on the Western Australian coast. The paucity of *Amphisorus* and absence of related *Marginopora* in the Holocene sediment, suggest that seagrass stands may have been rare in the Gulf throughout the Holocene.

Acknowledgements: Samples for this study were made available by the Australian Institute of Marine Science, and were collected by the ship-board scientists on AIMS cruises 669 and 672 during September-October 1994. Sedimentological and bathymetric data were provided by A Orpin and K Woolfe of the Department of Earth Sciences, James Cook University of North Queensland. S Revets provided taxonomic advice on some of the species

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Abundance of arthropods in tree canopies of *Banksia* woodland on the Swan Coastal Plain

R A Tassone^{1,2} & J D Majer²

¹Entomology Section, Agriculture Western Australia, South Perth WA 6151

²School of Environmental Biology, Curtin University of Technology, Kent Street, Bentley, WA 6845
email: imajerj@info.curtin.edu.au

Manuscript received January 1997, accepted May 1997.

Abstract

Canopy arthropods and foliar nutrients were quantified during summer for *Banksia menziesii*, *B. attenuata*, *B. ilicifolia* and *Nuytsia floribunda* within a low woodland site at Jandakot Airport on the Swan Coastal Plain, Western Australia. Foliar nutrients were higher for *N. floribunda* than any of the *Banksia* species. *B. ilicifolia* differed from the other two banksias in having lower nitrogen and phosphorus but higher potassium. Invertebrate densities were also higher for *N. floribunda* than any of the *Banksia* species, while densities on the three *Banksia* species were relatively similar, albeit with a few predominantly phytophagous taxa having a higher density on *B. ilicifolia*. These trends provide evidence that, as in other ecosystems where this has been studied, differing arthropod loads between tree species are related to variation in foliar nutrient levels. Tree usage by predominantly insectivorous birds may reflect the relatively low difference in arthropod loads between the three *Banksia* species and an uneconomic strategy of seeking out low-density *N. floribunda* trees.

Introduction

Invertebrates are an ubiquitous component of most terrestrial ecosystems and a key element in the energy flow and nutrient turnover within a community. Arboreal invertebrates may function as major herbivores, pollinators, parasites and predators (Majer & Recher 1988), and are themselves an important food resource for vertebrates. The dynamics of bird communities are closely linked to the abundance and diversity of invertebrates, with insectivorous avifauna responding to variations in the abundance of prey (Recher *et al.* 1991). Studies in open eucalypt forests of New South Wales by Recher & Majer (1994) showed that the abundance and biomass of invertebrates on eucalypts selected by birds were greater than on less preferred species. Similar invertebrate-driven preferences in tree usage by birds exist in wandoo (*Eucalyptus wandoo* Blakely) woodland (Majer & Recher 1988) and jarrah (*E. marginata* Donn ex Smith) forest (Recher *et al.* 1996) in Western Australia.

In south-western Australia there is a distinct seasonality of climatic patterns and there are also considerable differences in weather patterns between years. These variations, coupled with soil nutrients, moisture and the effects of fire, result in the local vegetation having variable levels of invertebrates. Recher *et al.* (1996) described these forests and woodlands as fluctuating environments, which possess significant temporal and spatial variation in invertebrates.

Another variable influencing invertebrates in tree canopies is vegetation type. This study provides data for invertebrate densities on tree canopies of *Banksia* woodland at Jandakot Airport on the Swan Coastal Plain. It complements data on canopy arthropods in other

Western Australian ecosystems, ranging from mallee (Recher *et al.* 1993) to wandoo woodland (Majer & Recher 1988, Majer *et al.* 1996) to jarrah forests (Majer *et al.* 1990, 1994).

At present, natural bushland covers approximately 237 ha of Jandakot Airport and most of this is in a relatively undisturbed state (Milewski & Davidge 1981). In 1993, a draft environmental impact statement for additional development of aviation facilities, extraction of silica sand, and construction of a commercial estate (Anon 1993) proposed that 96 ha (40.5%) of the airport bushland be conserved. The significance of urban bushland remnants to vertebrate fauna has been noted by How & Dell (1994) who have conducted surveys in this region. In view of this, it is important to gather information on how the area caters for the feeding requirements of insectivorous vertebrates, such as birds.

Methods

Study site

The study was undertaken at Jandakot Airport (32°6'S, 115°53'E), 18 km south of the centre of Perth and 9.5 km east of the coast, in the City of Cockburn. The vegetation of this region of the Swan Coastal Plain is broadly classified as "low woodland" over "heath" and the airport has mainly mixed woodlands of the Proteaceae, *Banksia menziesii* R Br, *B. attenuata* R Br and *B. ilicifolia* R Br (Milewski & Davidge 1981). These banksias can be co-dominant, but vary widely in relative abundance. The study site is located within the Bassendean Dune system in a swale that retains high soil moisture throughout winter. This grey soil is a heavily leached sesquioxide podsol and is acidic (McArthur & Bettenay 1960). The mean annual rainfall at Jandakot

Airport is 802 mm, with most rain falling between May and August.

Sampling was carried out within a woodland area measuring 100 m by 130 m. The site was 15 m from the edge of the woodland, and had a 1.5 m sand bank between this edge and an access road. The area was adjacent to the study site used by the Western Australian Museum (R A How & J Dell, *pers comm*) for determining the significance of remnant urban bushland to reptile and other fauna. We sampled the three *Banksia* species and also *Nuytsia floribunda* (Labill) R Br ex Fenzl (Loranthaceae), which was scarce and contributed less than 2% to the tree cover. Tree canopy cover was 47%, and averaged 6 - 7 m in height. The dense understorey was dominated by the 2 m tall shrub, *Regelia ciliata* Schauer (Myrtaceae), which had a patchy distribution throughout the study site, and also by grass trees, *Xanthorrhoea preissii* Endl (Xanthorrhoeaceae). The ground cover consisted of undershrubs and perennial herbs. An additional tree species, *Eucalyptus tottiana* F Muell (Myrtaceae), was also present, but was so sparsely distributed that it was not included in this study.

All three *Banksia* species can be trees up to 10 m in height. The leaves of *B. menziesii* are dull green and very rigid, 10 - 40 mm wide and 80 - 250 mm long (Marchant *et al.* 1987). The conspicuous flower heads (held above the foliage) are usually pink or red, occurring mainly in February to August. The leaves of *B. attenuata* are more crowded than *B. menziesii* and much narrower, being 5 - 15 mm wide, 40 - 270 mm long, and strongly serrated. The conspicuous flower heads are bright yellow, appearing from September to December. The common name holly-leaved banksia aptly describes *B. ilicifolia*, with its dark green leaves; they are 20 - 40 mm wide and 30 - 90 mm long, elliptical with an undulating edge, and the leaves are slightly serrated with each tooth possessing a spine. The flower heads are cream, turning deep pink with age. The flowers appear throughout the year, but peak in spring. *N. floribunda* is a tree up to 10 m high, that parasitises the roots of surrounding plants. The glabrous leaves are long (40 - 100 mm), narrow (3 - 8 mm) and thick. This tree has masses of orange flowers, which occur from October to January. To touch, the leaves of *N. floribunda* are much less sclerophyllous than the leathery *Banksia* leaves. When bent, *B. menziesii* and *B. attenuata* leaves crack and split, unlike *B. ilicifolia* whose leaves are more supple.

Sampling

The proportional composition of tree species within the canopy was assessed above 400 vertical sighting points taken at regular distances along transects throughout the study site.

Arthropods were sampled from the canopy of the three *Banksia* and *N. floribunda* during early summer (December 1994). We sampled trees which were not in flower, since we were primarily interested in foliage-associated arthropods. The number of trees sampled was dictated by their availability in the study site. Consequently, 20 each of *B. menziesii* and *B. attenuata*, 10 of *B. ilicifolia* and four of *N. floribunda* were sampled. The height and crown diameter was recorded for each tree. Mature foliage was collected from 10 individuals of each

species for subsequent analysis of nutrients. Leaf material was dried at 60 °C for 48 hours and ground to a fine powder prior to analysis.

Cotton, funnel-shaped nets with a sampling area of 0.5 m² were used to collect the chemical knockdown samples. Each net was fitted with a sleeve that held a 100 ml plastic tube. Within a given tree, five nets were suspended at different heights below the canopy foliage. Net positions were selected to equalize the amount of foliage (determined by visual inspection) in the column directly above the nets. Nets were positioned in the morning (0800 h), one hour prior to spraying, to allow disturbed invertebrates to return.

The canopy above each net was sprayed with synthetic pyrethrin pesticide, synergised with piperonyl butoxide, using a motorized-knapsack mist-blower. Spraying was done only during dry and calm conditions. Two litres of diluted (0.2%) pesticide was used per tree, and trees were left for at least 30 minutes to allow silk-attached invertebrates to drop into nets. The canopy was then shaken to dislodge remaining invertebrates and specimens were brushed into the collecting tubes and preserved in 70% ethanol prior to sorting and counting to ordinal level.

The numbers of invertebrates caught could be influenced by the amount of foliage above each net. To obtain a measure of this, we cut three 1 m long branches (measured from growing tip backwards) from each tree species and counted the number of leaves on each branch. Twenty leaves of each species were then removed and their surface area measured using a computer-based planimeter. This enabled a measure of the area of foliage on a 1 m branch to be calculated.

Data analysis

Following sorting, the number of animals within each taxon was summed for the five nets placed within each tree. Mean and standard error of the numbers of each invertebrate taxon on each tree species were then calculated. Three comparisons were made; (1) between the three *Banksia* species for each invertebrate taxon; (2) between the three *Banksia* species for all taxa that were significantly different; and (3) between the four sampled tree species for each invertebrate taxon. Analyses were restricted to the common invertebrate taxa, those occurring in >65% of the samples. *N. floribunda* was excluded from comparisons (1) and (2) because of the low number of trees sampled. Comparison (1) was performed by univariate analysis of variance (ANOVA) and those means which differed significantly were detected using Tukey's pairwise comparisons ($P < 0.05$). Comparison of *Banksia* species for each invertebrate taxon required natural log transformations of the data due to the high degree of variability or the presence of zeros. Comparisons (2) and (3) involved ranking the invertebrate taxa and comparing these ranks using Kendall's coefficient of concordance.

Foliar samples from each tree were analysed for total nitrogen, phosphorus and potassium (see Majer *et al.* 1992 for methodology). The variation in nutrient levels between the four sampled tree species was analysed by univariate analysis of variance (ANOVA) and those means which significantly differed were detected using Tukey's pairwise comparisons ($P < 0.05$). Standard

deviations were relatively homogeneous, indicating that transformations were unnecessary.

Results

In terms of cover, *B. attenuata* was the most dominant species (70% of projected foliage cover), followed by *B. menziesii* (20% of projected foliage cover) and *B. ilicifolia* with 7% of projected foliage cover (Table 1). Table 1 also indicates that *B. ilicifolia* was the smallest tree species sampled, having up to a 2 m crown diameter. The single main stem of this species had many branchlets that formed a cover of dense foliage around its stem. The large crown diameter of *N. floribunda* was in part associated with the tendency of this species to have more than one main stem. *B. attenuata* and *B. menziesii* had similar canopy structure, with the diameter (3.0 - 3.5 m) and height above the ground (6.5 - 7.0 m) of their crowns being similar. The area formed by the crown of *N. floribunda* (17.3 m²) was twice as large as *B. menziesii* (7.3 m²) and *B. attenuata* (9.5 m²), and approximately six times larger than *B. ilicifolia* (3.2 m²). *N. floribunda* supported by far the most leaves per metre of branch, followed by *B. attenuata*; *B. menziesii* branches had the lowest number of leaves (Table 1). When leaf area was taken into account, *N. floribunda* branches supported the least foliage, *B. attenuata* the most, while the other two banksias were intermediate.

There were generally significantly higher levels of nitrogen, phosphorus and potassium within the leaves of *N. floribunda* than in the *Banksia* species (Table 2). Nitrogen and phosphorus are generally mobile nutrients within the plant, and their within-plant concentrations are usually correlated (Majer *et al.* 1992). This is a probable

explanation for the assayed leaves showing identical patterns of significance for nitrogen and phosphorus. *B. ilicifolia* had significantly lower levels of nitrogen and phosphorus but higher levels of potassium than the two other *Banksia* species. *B. menziesii* and *B. attenuata* exhibited no significant difference between their levels of nitrogen, phosphorus or potassium.

A total of 7 105 individual arthropods was obtained from the 54 tree canopies sampled. The invertebrate count was higher on *N. floribunda* than on any of the *Banksia* species (collected arthropods averaged 216 from *N. floribunda*, 182 from *B. ilicifolia*, and only 107 - 114 from *B. menziesii* and *B. attenuata* respectively). The F ratios for univariate ANOVA comparisons of the three *Banksia* species, together with means and standard errors for the data, are presented in Table 3. It is evident that the densities of only a few invertebrate taxa differ significantly between sampled *Banksia* species within woodland at Jandakot. These invertebrates are Acarina (mites), Blattodea (cockroaches), Homoptera (sucking bugs), Thysanoptera (thrips) and Neuroptera (lacewings) larvae. In almost all significant differences, numbers were significantly higher on *B. ilicifolia* than *B. menziesii* and *B. attenuata*. The exception was for Blattodea, where *B. ilicifolia* and *B. attenuata* had similar but higher densities than *B. menziesii*. Levels of the various invertebrate taxa generally did not significantly differ between *B. attenuata* or *B. menziesii*, although Acarina were significantly more abundant on *B. menziesii* and, as mentioned, Blattodea were significantly more abundant on *B. attenuata*.

Despite these abundance differences, almost the same variety of taxa were found on the four tree species. Overall, arthropods from 20 orders of insects (Heteroptera and

Table 1

Crown diameter and height (n = 10), the proportional composition of the overstorey, mean leaf area (n = 20), and the number and area of leaves along 1 m branches (n = 3) of sampled tree species in the *Banksia* woodland study site at Jandakot Airport during December 1994. Values are mean ($\pm$ se).

Species	Crown diameter m	Tree height m	Percentage canopy (%)	Leaf area cm ²	Number of leaves on 1 m branch	Leaf area on 1 m branch (cm ²)
<i>Banksia attenuata</i>	3.5 $\pm$ 0.2	7.0 $\pm$ 0.2	69.9	9.4 $\pm$ 0.4	979.7 $\pm$ 7.7	9256.9
<i>Banksia menziesii</i>	3.0 $\pm$ 0.2	6.7 $\pm$ 0.2	19.9	25.6 $\pm$ 0.6	274.3 $\pm$ 5.3	7021.9
<i>Banksia ilicifolia</i>	2.0 $\pm$ 0.3	6.4 $\pm$ 0.4	6.8	14.5 $\pm$ 0.4	490.7 $\pm$ 6.7	7124.0
<i>Nuytsia floribunda</i>	4.5 $\pm$ 0.4	6.7 $\pm$ 0.4	1.7	2.1 $\pm$ 0.2	2023.7 $\pm$ 15.8	4236.3
Others	-	-	1.7	-	-	-

Table 2

Nutrient levels ($\mu\text{g g}^{-1}$) within tree foliage (n = 10) from *Banksia* woodland at Jandakot Airport during December 1994. The means ($\pm$ se) of are shown with level of significance (P) between tree species; different superscript letters indicate that means differ significantly using univariate analysis of variance (ANOVA)

Total nutrient	Species				Nutrient comparison	
	<i>B. menziesii</i>	<i>B. attenuata</i>	<i>B. ilicifolia</i>	<i>N. floribunda</i>	F Value	P
Nitrogen	5353.0 $\pm$ 6.6 ^b	5540.0 $\pm$ 6.4 ^b	3914.0 $\pm$ 8.3 ^c	6746.0 $\pm$ 9.3 ^a	34.5	< 0.05
Phosphorus	209.5 $\pm$ 1.7 ^b	200.5 $\pm$ 1.7 ^b	157.5 $\pm$ 1.8 ^c	434.5 $\pm$ 2.0 ^a	141.2	< 0.05
Potassium	1680.0 $\pm$ 6.2 ^b	2065.5 $\pm$ 4.0 ^b	2602.5 $\pm$ 7.2 ^a	2471.0 $\pm$ 7.5 ^a	9.2	< 0.05

Table 3

Numbers of invertebrates per tree, sampled by pyrethrin knockdown of *Banksia* woodland canopy at Jandakot Airport during December 1994. The number of invertebrates per tree was based on five 0.5 m² nets within the canopy. Best ranks are assigned to all taxa and also the five taxa where significant differences occurred. Means ($\pm$ se) for the three *Banksia* species were compared where possible using a univariate analysis of variance (ANOVA) and those means which differ significantly are indicated by different superscript letters. Taxa with significant differences between banksia species are indicated in bold. Ranks compared using Kendall's Coefficient of concordance. NS = not significant.

Class	Taxon	Species				Tree comparison		
		<i>B. menziesii</i> n = 20	<i>B. attenuata</i> n = 20	<i>B. ilicifolia</i> n = 10	<i>N. floribunda</i> n = 4	F Value	P	
Arachnida	Pseudoscorpionida	0.2 ± 0.2	0.3 ± 0.2	0.1 ± 0.2	4.8 ± 0.9		-	
	Acarina	23.7 ± 1.1 ^b	11.5 ± 0.7 ^c	74.8 ± 2.5 ^a	22.8 ± 2.2	15.4	< 0.05	
	Araneae	8.0 ± 0.5	12.1 ± 0.6	10.0 ± 0.8	22.0 ± 1.8		NS	
Crustacea	Isopoda	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0		-	
Collembola		0.5 ± 0.2	0.2 ± 0.1	1.1 ± 0.5	0.3 ± 0.4		-	
Insecta	Thysanura	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	3.0 ± 0.6		-	
	Blattodea	0.2 ± 0.1 ^b	1.2 ± 0.3 ^a	1.1 ± 0.3 ^a	1.8 ± 0.6	5.1	< 0.05	
	Plecoptera	0.1 ± 0.1	0.3 ± 0.2	0.2 ± 0.2	1.0 ± 0.6		-	
	Mantodea	0.2 ± 0.1	0.2 ± 0.1	0.1 ± 0.2	0.5 ± 0.4		-	
	Isoptera	0.5 ± 0.2	0.4 ± 0.2	0.8 ± 0.4	2.5 ± 0.9		-	
	Orthoptera	0.1 ± 0.1	0.0 ± 0.0	0.1 ± 0.2	0.3 ± 0.4		-	
	Pscoptera	3.0 ± 0.4	2.2 ± 0.3	5.6 ± 0.7	54.0 ± 2.3		NS	
	Hemiptera	Homoptera	2.7 ± 0.4 ^b	4.4 ± 0.4 ^b	9.1 ± 1.1 ^a	12.5 ± 1.6	4.2	< 0.05
		Heteroptera	5.7 ± 0.6	4.7 ± 0.5	8.6 ± 0.8	3.3 ± 1.0		NS
	Thysanoptera		9.2 ± 0.5 ^b	12.8 ± 0.7 ^b	24.6 ± 1.4 ^a	8.5 ± 1.7	3.3	< 0.05
	Neuroptera	adults	0.1 ± 0.1	0.5 ± 0.3	0.3 ± 0.3	0.5 ± 0.5		-
		larvae	1.0 ± 0.3 ^b	1.0 ± 0.3 ^b	2.6 ± 0.4 ^a	7.3 ± 1.6	6.7	< 0.05
	Coleoptera	adults	12.1 ± 0.6	18.3 ± 0.7	14.5 ± 1.2	37.0 ± 3.6		NS
		larvae	12.3 ± 0.7	11.3 ± 0.6	6.8 ± 0.6	3.0 ± 1.1		NS
	Mecoptera		0.5 ± 0.3	0.6 ± 0.3	0.0 ± 0.0	0.0 ± 0.0		-
	Diptera	adults	1.8 ± 0.3	1.8 ± 0.3	3.2 ± 0.6	6.5 ± 1.0		NS
		larvae	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0		-
	Lepidoptera	adults	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.8 ± 0.5		-
		larvae	1.1 ± 0.3	1.0 ± 0.3	0.2 ± 0.2	0.0 ± 0.0		NS
	Hymenoptera	ants	16.6 ± 0.9	17.9 ± 1.1	7.5 ± 1.2	7.8 ± 1.4		NS
		others	7.5 ± 0.4	11.9 ± 0.8	10.7 ± 0.8	16.5 ± 1.3		NS
Total invertebrates		106.7	114.4	182.0	216.3			
Best rank (All taxa)		4	2	3	1			
Arachnida	Acarina	2	3	1	-			
Insecta	Blattodea	3	1.5	1.5	-			
	Hemiptera	Homoptera	2.5	2.5	1	-		
	Thysanoptera		2.5	2.5	1	-		
	Neuroptera	larvae	2.5	2.5	1	-		
Best rank (Significant taxa)		3	2	1	-			

Homoptera counted as one order), arachnids, crustaceans and collembolans were collected, with 18 sampled on *N. floribunda*, 17 on *B. attenuata* and *B. ilicifolia*, and 20 on *B. menziesii*. The most abundant invertebrate order on the four tree species was Acarina, with over 1540 individuals recovered (22% of total). Along with Acarina, Coleoptera (beetles) and Hymenoptera (ants, wasps, sawflies and bees) dominated the numbers of invertebrates collected from Jandakot. Of the 20 orders sampled, these three composed 61% of the total number of invertebrates.

The numbers of invertebrates in each taxon were ranked across tree species for all taxa and also for those taxa which exhibited significant differences (Table 3). In the first of these rankings, *N. floribunda* ranked as having the most abundant invertebrate fauna, followed by *B. attenuata*, *B. ilicifolia* and finally *B. menziesii*. This ranking was not significant (Kendall's coefficient of concordance; $P > 0.05$), although it was in partial agreement with the ordering of total invertebrate counts in that *N. floribunda* was ranked the highest and *B. menziesii* the lowest; the

other two *Banksia* sp. were ranked as intermediate. When only those invertebrates with significant differences on *Banksia* species were ranked (on the basis of their ordering in the ANOVA analysis), *B. ilicifolia* had the most individuals, while *B. attenuata* was only marginally ranked higher than *B. menziesii*.

Discussion

The higher abundance of invertebrates on the canopy of *N. floribunda* than on that of the *Banksia* species supports the conclusions from other studies that invertebrate densities are higher in canopies of tree species with higher foliar nutrient levels (Majer *et al.* 1992), although it is not possible to test this statistically due to the low sample size. The possibility that higher invertebrate densities can be associated with greater amounts of foliage can here be eliminated as *N. floribunda* was the species with the lowest area of leaves above the sampling nets.

As with *N. floribunda*, the densities of invertebrates on the three *Banksia* species were unrelated to foliage area above the nets. The densities of invertebrates in canopies of the three *Banksia* species were all relatively similar. *B. menziesii* and *B. attenuata* had almost identical foliar nutrient levels, so it is consistent that the density of invertebrates on these two species was similar. The position of *B. ilicifolia* in the invertebrate rankings was equivocal, since its foliar nutrient levels were lower in nitrogen and phosphorus, but higher in potassium than those of the other two banksias. Usually it is the levels of nitrogen which correlate with invertebrate levels, particularly herbivores, presumably because this reflects the protein content of the diet (see references in White 1969; Morrow 1983). Phosphorus and potassium levels may also reflect some aspects of the nutritional quality of the foliage, so possibly the effects of higher potassium cancels out the effects of lower levels of the other two nutrients.

Certain taxa do exhibit significant differences between the *Banksia* species and four of these taxa (Acarina, Blattodea, Homoptera and Thysanoptera) contain species which derive their nutrients directly from live or decaying leaves. The fact that they reach greatest abundance on *B. ilicifolia* suggests that some taxa may be responding to the higher levels of potassium in leaves of this species. These trends therefore provide evidence supporting the fact that, as in other ecosystems where this has been studied, differing arthropod abundance's (Recher *et al.* 1996) and richness levels (Majer *et al.* 1994) between tree species may be related to foliar nutrient levels. An alternative possibility is that the higher foliage density on *B. ilicifolia* may create a more favourable microclimate for arthropods.

The other studies on canopy arthropods elsewhere in Australia (see Introduction) used identical procedures, with the exception that 10 nets were used to sample the overstorey trees. How do the levels of invertebrates compare with other trees in Western Australia? If values are expressed as mean number of invertebrates per net, then the *Banksia* species support similar levels of arthropods to *E. marginata* and *E. calophylla* Lindley (marri) trees sampled during the same season in the

nearby jarrah forest (Recher *et al.* 1996). Levels of invertebrates on *N. floribunda* were considerably higher than those normally present on local *Eucalyptus* species. Arthropod levels on all tree species in the present study were higher than on trees in the more arid mallee (Recher *et al.* 1993) and wheatbelt woodland sites (Majer & Recher 1988, Majer *et al.* 1996), suggesting the possible existence of a gradient of canopy arthropod densities with increasing rainfall.

Tree usage by insectivorous birds was recorded in the same site during the period when invertebrates were sampled through until September 1995 (P Kirkpatrick, School of Environment Biology, Curtin University, unpublished data). When the proportion of feeding observations was assigned to the various tree species, it was found that values reflected the proportional composition of the overstorey for each tree species. Thus, insectivorous birds at Jandakot do not appear to be selecting particular tree species as foraging substrates, but rather use the various species of tree in a random manner. The absence of any apparent selection of tree species by insectivorous birds is consistent with the *Banksia* species supporting relatively similar invertebrate loads. The absence of any selection for *N. floribunda*, despite its higher nutrient loads and invertebrate numbers, is surprising. It is possible that its low density within this ecosystem means that birds do not find it economical to seek out this tree species. Another possibility is that birds may find it difficult to probe for invertebrates amongst the dense foliage of this species.

These findings suggest that, on a unit area basis, *Banksia* woodland provides similar amounts of food for canopy-feeding insectivorous birds as does the jarrah forest in the Darling Ranges. Indications are that, in contrast to the jarrah forest, insectivorous bird richness is low at Jandakot Airport and that some species are no longer present (How & Dell 1993). Probably the fragmentation of the woodlands of the Swan Coastal Plain, and the reduction in area of this habitat, has reduced the available feeding areas for tree-dependent birds and this has resulted in the local extinction of some species. The presence of this array of invertebrates in the canopies of *Banksia* species and *N. floribunda* presents a compelling case for maintaining this sizeable remnant of native woodland at Jandakot Airport.

Acknowledgments: We would like to thank K Flecknell and the Federal Airports Corporation for permission to use the Jandakot Airport site and also P Kirkpatrick, R P Tassone and E Kostas who assisted with field work. N Keals and M J de Sousa Majer helped with sorting of arthropod material and K McGregor, J O'Neil and M Costigan of the Department of Ecosystem Management, University of New England, performed the nutrient analyses. P Groom assisted with the leaf area measurements and R How, B Lamont, J Scott and an anonymous referee kindly commented on an earlier draft of this paper.

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The Royal Society of Western Australia Medallists, 1997

Dr Ernest Hodgkin, OAM



Ernest Hodgkin was born in Madagascar in 1908, and subsequently grew up in the United Kingdom. He graduated in 1930 with a BSc (Hons) in Zoology from the Victoria University of Manchester. Following his graduation, he was employed as an entomologist for the Institute of Medical Research for the Federated Malay States, where he

worked on arthropod vectors of malaria, filariasis and rickettsial disease until 1942, when he was interned in Singapore as a civilian Prisoner of War.

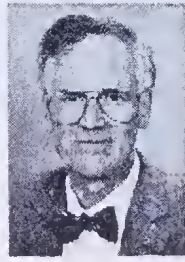
After his release from internment in 1945, he was reunited with his family, who had moved to Perth. Ernest was appointed a lecturer in the Department of Zoology at the University of Western Australia in 1946, where he remained until 1973 having been promoted to Associate Professor. In 1950, he gained a DSc from UWA on "The transmission of malaria in Malaya", and has published 14 papers on this subject. From the mid-1950s he carried out research on the ecology of invertebrate fauna of freshwater, estuaries and rocky shores, and coastal geomorphology. He supervised the research and training of a series of research students and published 28 papers in this area up to 1974. Many of his students have gone on to positions in Universities, Government Departments or private consultancies.

From 1955 to 1958 Ernest was also a Trustee of the Western Australian Museum, being Vice-Chairman from 1960-1981 and Chairman from 1982-1983.

On retiring from his University position in 1974 at the age of 65, Ernest has continued a remarkable contribution to science in Western Australia. From 1974 to 1996 he was Environmental Consultant at the Department of Conservation and Environment, and the Environmental Protection Agency, when he co-ordinated team research studies of the Blackwater River and on eutrophication in the Peel-Harvey estuarine system. He published a further 25 papers on the Blackwood Estuary, the Peel-Harvey and other Estuaries, including the "Estuarine Studies Series" published by the EPA. This series sets out geomorphological and biological characteristics of the 21 estuaries from Augusta to Esperance. From 1989-1996 he was environmental advisor to the Department of Environmental Protection, when he provided advice on the management of Culham Inlet and other estuarine systems. In 1996 he co-authored the book "Estuaries of the South Coast".

In recognition of his outstanding work, Ernest was awarded the Order of Australia Medal (OAM) in 1983, and the Royal Society of Western Australia is pleased to acknowledge his remarkable contributions to various aspects of knowledge of estuaries in the south-west of the State both before and since that time, by the award off the Royal Society of Western Australia Medal for 1997.

Dr Arthur McComb



Arthur McComb was born in Melbourne in 1936. He attended the University of Melbourne where he graduated in 1956 with a joint major in Botany and Zoology, and an Exhibition and First Class Honours in Botany. This was followed by an MSc from the University of Melbourne in 1959. With the help of a Royal Commission for the Exhibition of 1851

Overseas Scholarship, he undertook his PhD research at the University of Cambridge, which was completed in 1962.

Arthur returned to Australia with a lectureship at the University of Western Australia (1963-1967), and was promoted to Senior lecturer in 1967. He spent two years carrying out research abroad, first in 1969 as a Research Associate at the Atomic Energy Commission, Michigan State University, and then in 1976 as an Honorary Research Fellow at the University of Leicester. Promotions followed, first to Associate Professor in 1977 and Head of the Botany Department at UWA (1981-1986), then to Professor of Environmental Sciences at UWA (1981-1986), and Professor of Environmental Sciences at Murdoch University (1989-present). From 1982 (until present), Arthur has been Joint Director of the Centre for Water Research.

His work has been in two major areas, the control of plant growth by internal factors, and the control of plant growth by the environment. The first area involved plant growth regulators (gibberelins). As a logical extension to this work, Arthur's interests began to move towards ecological aspects of plant physiology, particularly in relation to annual Western Australian plants, but also studies on resins produced by native species, that have similar structures to gibberelins. The major part of Arthur's work has been on control of growth in aquatic plants, particularly understanding the fundamental processes that control plant biomass in aquatic systems. This has been of considerable management significance, especially in relation to the accession of nutrients from catchments and their effects in receiving waters.

Publications include more than 120 scientific papers has written or edited six books. Arthur has supervised some 30 PhD students. His former students are spread throughout Australian science, in Universities, State Government Departments and in private consulting firms.

Service to the scientific community includes President of the Royal Society of Western Australia (1978), on the Scientific Advisory panel of the World Wildlife Fund (1984-1986), Deputy Chair then Chair of the WA National Parks and Nature Conservancy Authority (1985-1995), Chair of the WA Lands and Forests Commission (1988-1998), and President of the Ecological Society of Australia (1987-1988).

Arthur McComb has had a seminal influence on a generation of researchers. The Royal Society of Western Australia is pleased to honour his contribution to Western Australian and world science by the award of the Royal Society of Western Australia Medal for 1997.

[MGK Jones, President, RSWA, July 1997]

OBITUARIES

William Harold Cleverly

William Harold Cleverly, known to everyone as 'Bill', died on 19 April 1997, shortly after his 80th birthday. Born in Guildford, Western Australia, on 25 January 1917, he joined the Royal Society of Western Australia in 1938 and was later to become a regular contributor to the Society's Journal. In recognition of his contribution to science in Western Australia, Bill was made an Honorary Member of the Society in 1982. Bill graduated from the University of Western Australia in 1939 with a Bachelor of Science degree in Geology. An arduous correspondence course in mathematics with the University of Western Australia eventually saw him awarded a BA degree in 1951.

Known throughout the world for his work on Australian meteorites and tektites, Bill's early work was more geological. In 1939, he joined the North Australia Survey. During the early years of World War II, he carried out geological surveys of Queensland, mainly on the Atherton Tableland. In 1941 he returned to Western Australia to take up a short-lived appointment as Science Assistant at the Western Australian School of Mines (WASM, now part of Curtin University of Technology) in Kalgoorlie, before war service as an ammunition examiner with the AIF between 1942-46 on Borneo and other islands.

Following the war, Bill returned to Kalgoorlie to resume his post at the School of Mines and to settle down with his wife Evelyn. In 1947 he was appointed Lecturer and Head of the Geology Department at the WASM, the position he held until his retirement in 1977. It was during this period that his interest in meteorites and tektites increased. The 1960's saw the recognition of the arid zone of Western Australia, particularly the Nullarbor Region, as a potential source of meteorite finds. Together with his great friend, the late Keith Quartermaine, Bill made many forays into the Nullarbor to search for meteorites and tektites, and investigated many reports of meteorite falls and finds throughout the Goldfields. He also sparked an interest in meteorites in the late John Carlisle who subsequently collected many meteorites from the Nullarbor. Consequently, during the period 1960-1974 the number of meteorites known from Australia increased by 57, with the largest contribution coming from the Western Australian Nullarbor. During the 1960's alone, nearly a tonne of meteoritic material passed through the WASM into its collection, or via the School into other collections. This material included 37 new meteorites representing an addition of about 2% to all meteorites known in the world at that time. Together with colleagues such as Brian Mason, Joe McCall and John de Laeter, and aided by Evelyn, Bill documented and described this wealth of new meteoritic and tektite material. In addition to his work at the WASM, Bill was one of the longest serving members (1966-1987) of the Meteorite Advisory Committee of the Western Australian Museum.

As Curator of the Museum attached to the WASM from 1972-1977, Bill also had the job of caring for the collection, including meteorites and tektites, that had

been so enriched by his work. During twenty years of retirement, as an Honorary Research Fellow (1977-97) at the WASM, and as an Honorary Associate of both the Western Australian (1966-97) and South Australian (1977-97) Museums, Bill's scientific output never waned, and he published many papers on meteorites and tektites. Overall, he published more than 40 scientific papers and popular articles, including twelve as first author and one as a co-author in the Journal of the Royal Society. His meticulous and systematic work on the shapes and size distribution of tektites in Australia remains as a valuable contribution to science. Last year, while on one of his regular tektite hunting expeditions with Evelyn, Bill suffered a stroke and died in hospital shortly after. On a personal note, all who knew him will remember his warm, friendly nature, wonderful turn of phrase, and great sense of humour. His tall, gentlemanly figure will be greatly missed in the Goldfields.

[Alex Bevan, Department of Earth and Planetary Sciences, Western Australian Museum]

Brian John Grieve

Professor Brian Grieve, long-time member of the Royal Society of Western Australia, passed away on 5 September 1997, aged just over 90. Although a native Victorian, Brian Grieve became so much part of the botanical scene in Western Australia that he was readily accepted as a Sandgroper. Born in Allans Flat on 15 August 1907, he was educated at Williamstown High School and the University of Melbourne. In 1929 he gained First Class Honours in Botany, and the following year an MSc. Receiving an 1851 Exhibition, he studied for a PhD at the University of London in 1930-31, then returned to take up a lectureship in Botany at the University of Melbourne. He again spent two years in Britain in 1938-39, studying mycology at Cambridge. Early in the Second World War he served in the Royal Australian Naval Reserve but then returned to the University to investigate fungal contamination of field glasses in New Guinea.

Brian moved to Western Australia at the start of 1947 to become head of the Botany Department at the University of Western Australia. At the time there was one other lecturer and two graduate assistants. He set about building up both the Department and the courses offered. By 1957 the Department had grown to the extent that it was given a Chair, and Brian became the Foundation Professor. As staff and student numbers increased, the old wooden buildings (originally part of 'Tin Pot Alley' in Irwin Street in the City where the University was housed until 1930) became quite inadequate, and Brian planned the move to a new building which opened in 1969. The greatest strength of his contribution was the breadth of botanical subjects offered—general botany, anatomy, physiology, genetics, biosystematics, ecology, mycology and other cryptogams, systematics. Hundreds of students who passed through the Department have gone on to make significant contributions in their fields.

His own research turned towards the physiology of native plants, especially water relationships, laying a firm foundation for others to build on. He joined the Royal Society in 1948, and at the end of his first term as President in 1953, his address was on 'The physiology of sclerophyll plants' (*J Royal Soc Western Australia* 39:31-45, 1955). He was President again in 1970-71, closing this term with 'Botany in Western Australia: a survey of progress 1900-1971' (*J Royal Soc Western Australia* 58:33-53, 1975). In 1975 he was made an Honorary Life Member, and in 1979 was awarded the Society's Medal. In 1983 he delivered the Nancy Burbidge Memorial Lecture to the Australian Systematic Botany Society. He served on many committees both within and outside the University, including the Kings Park Board from 1959 to 1978.

Among the public and systematists, Brian is best known for his painstaking work on the project conceived by William Blackall—the illustrated keys published as 'How to Know Western Australian Wildflowers'. Blackall prepared considerable manuscript material before his death in 1941. His family asked the University to complete the work, and the task fell to Brian Grieve. Part 1 was published with little amendment in 1954 (the first work published by the University's Press), but all later parts required increasing input, both to incorporate existing taxa and to interpolate new discoveries. Brian worked towards this goal for almost 50 years, always in addition to his other duties, and often during vacation. Fittingly, his role was recognised in the authorship of later parts as 'Grieve and Blackall' rather than 'Blackall and Grieve'. The latest revision is currently in press.

Brian never published a formal taxonomic paper, yet his contribution to systematics has been immeasurable, providing a means for identifying wildflowers and hence encouraging the interest of students and users alike.

Never one to push himself forward, Brian was respected with esteem and affection by colleagues and students for his gentleness, wisdom and compassion.

[A George, RSWA Council]

Clee F H Jenkins

Mr Clee Francis Howard Jenkins, naturalist, broadcaster, entomologist and supporter of the Royal Society of Western Australia, died on July 13th aged 89. He was born in Adelaide in 1908 where he received his education at St Peter's College, and joined the Western Australian Museum as a cadet in 1929. He was appointed as an entomologist in the Western Australian Department of Agriculture in 1933, and as Government Entomologist in 1939 then Chief of the Division of Biological Services (incorporating Entomology, Botany, Plant Pathology and Weeds and Seeds) of the Department of Agriculture. He graduated with a BA from the School of Science, University of Western Australia, in 1935 then a MSc in 1939.

His obituary entitled 'Death of a Gentleman', written by Keith McDonald and published in the *West Australian* (21st July 1997), well sums up Clee Jenkins and his life. He joined the Royal Society of Western Australia in 1929 and played a prominent role in all aspects of the Society for many years. From the humble beginning as Assistant Librarian, he served in Executive or on Council for more than 30 years; his various roles included Honorary Secretary, Vice-president (4 years), President of the Society (three times over a span of 34 years, in 1945, 1963 and 1979) and member of Council. He was the tenth recipient to be awarded the Kelvin Medal of the Royal Society of Western Australia in 1966 for exceptional service to the Society, for advancement of science in all of its branches, and for his personal achievement in his own field. He worked for the Department of Agriculture, mainly in the field of insect control, and his sound recommendations were responsible for eradication of many important insect pests; this work greatly benefited Western Australia. Clee Jenkins also made a distinguished contribution to Science by his enthusiastic encouragement and publicity of natural history and ornithology, where he played an exceptionally important role in promoting interest in the natural environment and its conservation.

Clee Jenkins began writing for the *West Australian* in 1937, and his articles on an amazing range of conservation and natural history subjects appeared each week from then up to the present time. He also wrote more than 1 000 articles for radio and TV broadcasting.

The Council and members of the Royal Society of Western Australia recognise the outstanding contributions of Clee Jenkins to promoting Science in Western Australia, and extend their condolences and best wishes to his family.

[MGK Jones, President, RSWA]

